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A Re-examination of Bidder's Classification of the Calcarea

WILLARD D. HARTMAN

LÉVI (1953, 1956, 1957) has suggested a new classification of the Class Demospongiae in which the importance of embryological characteristics is stressed. He presents evidence for a diphyletic origin of this class of sponges, with one line leading from *Halisarca*-like ancestors in which parenchymula larvae and viviparity are the rule, and another from *Oscarella*-like ancestors in which amphiblastula larvae and oviparity are found.

Lévi's suggestion brings to mind a parallel proposal made by Bidder (1898) for subdividing the Class Calcarea in part, at least, on the basis of the presence of amphiblastula or parenchymula larvae. And, whereas the embryological data cited by Lévi in reclassifying the Demospongiae seem to me to be in part inconsistent with morphological characters, the system set forth by Bidder for the Calcarea is supported by a constellation of both embryological and morphological characteristics.

In proposing his classification Bidder emphasized the differences which Minchin (1896) had pointed out between the genera *Clathrina* and *Leucosolenia*. The two genera may be compared as follows:

Clathrina

1. Regular, equiangular triradiate spicules present.[1] (See Fig. 1*B*.)
2. Optic axes[3] of the spicules nearly perpendicular to the walls of the sponge tubes.
3. Choanocytes with a spherical nucleus located basally in the cell.
4. Flagellum of the choanocytes arises independently of the nucleus. (See Fig. 2*A*.)
5. Parenchymula larvae. (See Fig. 4*B*, *C*.)
6. Triradiates are the first spicules to appear in larvae.

Leucosolenia

1. Triradiate spicules predominantly or exclusively sagittal[2] and inequiangular. (See Fig. 1*A*.)
2. Optic axes[3] of the spicules vary in orientation according to the distance from the oscular rim.
3. Choanocytes with a pear-shaped nucleus apical in position.
4. Flagellum of the choanocytes arises directly from the nucleus. (See Fig. 2*B*.)
5. Amphiblastula larvae. (See Fig. 4*A*.)
6. Monaxons are the first spicules to appear in larvae.

Bidder regarded Poléjaeff's (1883) subdivision of the Calcarea along physiological lines into Homocoela and Heterocoela as "no more satisfactory than classifying higher animals according to whether they walk, swim, or fly." He proposed to divide the Class Calcarea into two subclasses, the Calcaronea and the Calcinea. Additional characteristics separating these two groups may be mentioned. Bidder (1898, 1920*a*) has noted a difference

[1] Triradiates may be absent (as in *C. stolonifer* Dendy, 1891); when present, all or most of them are regular and equiangular.

[2] Two of the rays or two of the angles form a pair while the third differs in some way. Typically the oscular rays form a pair and the basal ray is longer or shorter; the angle between the oscular rays is usually larger than the remaining two which are coequal.

[3] Known for only a few species in each genus so far.

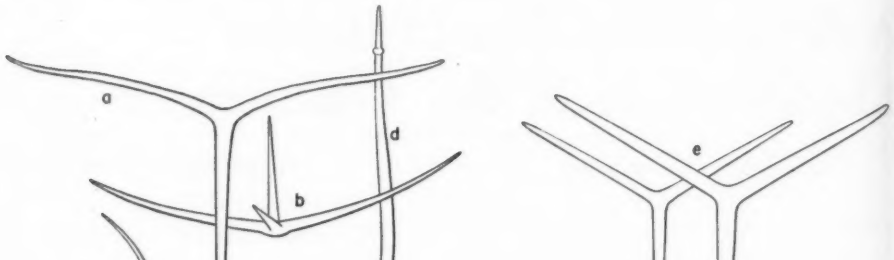

FIG. 1. Calcareous sponge spicules. *A. Leucosolenia complicata* (Montagu). *B. Clathrina coriacea* (Montagu). *a.* Sagittal triradiate; *b, c.* quadriradiates; *d.* monaxon; *e.* equiangular triradiate. (After Haeckel, 1872).

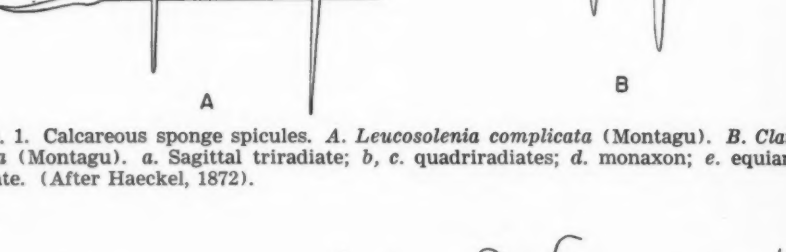

FIG. 2. Choanocytes, showing relationship of flagellum to nucleus. *A. Clathrina coriacea* (Montagu). Choanocytes of adult sponge with basal nuclei and independent flagella. *B. Leucosolenia complicata* (Montagu). Choanocytes of adult sponge with apical nuclei from which the flagella arise. *C. Leucosolenia botryoides* (Ellis and Solander). Flagellated cells of larva. *D. Clathrina blanca* (Miklucho-Maclay). Flagellated cells of larva. (After Minchin, 1909.)

in color and odor among species of the two subclasses. Most calcinean species "show varieties which are coral-red and sulphur-yellow" while in the Calcaronea these colors do not occur. The Calcinea have a very noticeable "aromatic" odor which is much less pronounced among the Calcaronea. Such characteristics can be highly useful in field studies. Bidder (1920*a*) presented evidence that the sperm cells of *Clathrina coriacea* may be amoeboid in contrast to the free-swimming sperm cells of *Leucosolenia* and *Sycon*. He postulated that the scent of calcinean sponges may arise from granules located around the ostia and may function as a chemical attractant for the creeping spermatozoans. These observations, which require confirmation and extension to other species, may eventually

help to bear out the distinctness of the two lines of calcareous sponges. Bidder (1898) also noted a difference in the structure of the prosopyles (pores leading into the flagellated chambers) in the two groups of Calcarea. In the genera *Leucosolenia, Sycon,* and *Leucandra* he described the pore cell (pylocyte) as lying at the bottom of a funnel-shaped depression or afferent canal, whereas in *Clathrina* he described an amoeboid pylocyte which perforates the entire sponge wall. Further comparative studies are needed to determine if these differences are consistent in the two subclasses.

Another possible difference concerns the nature of the mesogloea. Herlant-Meewis (1949) noted rows of small orcein-positive granules which represent very fine elastin fibers in the mesogloea of *Clathrina coriacea;* Jones (1956) was unable to find these structures in *Leucosolenia complicata,* in which orcein stains only the cell processes, spicule sheaths, and the crumpled epidermal layer. How general this difference may be has yet to be determined.

Still another difference between the Calcaronea and Calcinea concerns the extent of development of four curious cells in the larvae. Duboscq and Tuzet (1937, 1941, 1942) have described four cells distributed symmetrically around the third or fourth tier of flagellated cells above the equator in the amphiblastula larvae of *Sycon, Grantia,* and *Leucosolenia botryoides.* Structural details of these cells, which are arranged in the form of a cross, are shown in Figure 3. The cells degenerate in all cases before metamorphosis [4] and apparently function during the larval period as light receptors, or at least in some species of *Sycon.* These "cellules en croix" are characteristic structures of the amphiblastula larvae of the Calcaronea but fail to differentiate in the larvae of the Calcinea. Tuzet (1948) regards four cells with siderophilic regions found in the early cleavage stages of *Clathrina coriacea* as undifferentiated homologues of the "cellules en croix" of the Calcaronea (see Fig. 3*A*).

In the Calcaronea Bidder included *Leucosolenia* essentially as defined above, as well as the families Sycettidae, Grantidae,[5] Heteropidae, and Amphoriscidae, in all of which amphiblastula larvae occur and the nucleus of the choanocytes is distal, with the flagellum arising from the nucleus directly. In the Calcinea he placed the genus *Clathrina* as defined above together with the Leucascidae, Reticulatae (*Ascaltis* and *Ascandra*), and the Heteropegmidae (*Dendya* and *Heteropegma*), all of which have parenchymula larvae and basal nuclei in the collar cells, with the flagellum arising independently of the nucleus.

Tuzet (1948) restudied the development of *Leucosolenia botryoides* (Ellis and Solander) and *Clathrina coriacea* (Montagu), reaffirmed the embryological differences between them, and supported the re-establishment of the genus *Clathrina* as distinct from *Leucosolenia.* Jones (1954) has arrived at a similar conclusion as a result of his studies of the skeletal organization of *Leucosolenia complicata* (Minchin) and *Clathrina coriacea* (Montagu). The confirmation of the work of Minchin and Bidder offered by Tuzet and Jones would seem to justify a reconsideration of Bidder's classification of the Calcarea.

Dendy and Row (1913), in their revision of the Calcarea, rejected Poléjaeff's arbitrary classification of the class into Homocoela and Heterocoela and followed "much the same line of cleavage" as Minchin and Bidder. However, Dendy and Row considered Bidder's subdivision of the class into the subclasses Calcaronea and Calcinea to be "somewhat premature in the present state of our knowledge" and divided the class Calcarea "straightway into [ten] families." They pointed

[4] In *Sycon elegans* (Bowerbank) the cells are expelled before the larvae leave the parent sponge. See Duboscq and Tuzet, 1941.

[5] Bidder's spellings are used here.

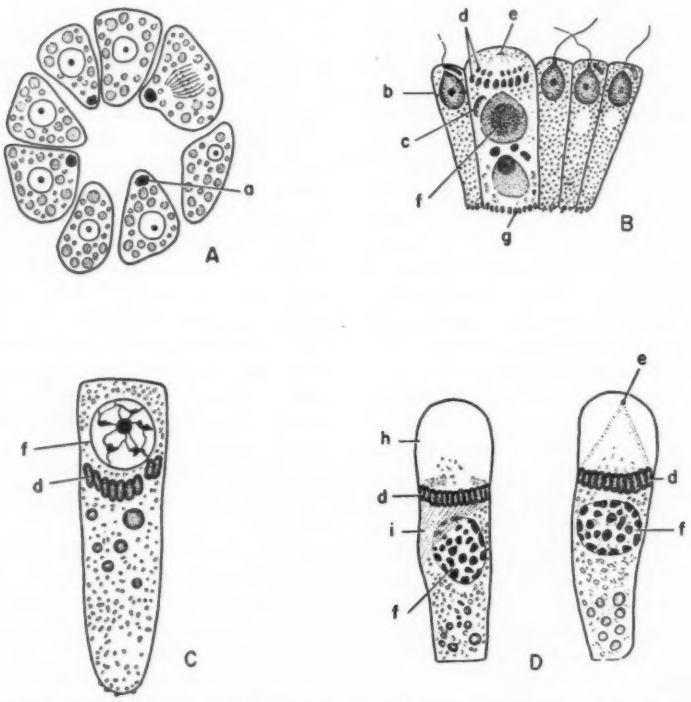

FIG. 3. "Cellules en croix." *A. Clathrina coriacea* (Montagu). Cross section through embryo at eight-cell stage, showing groups of siderophilic granules at inner ends of alternate cells. (After Tuzet, 1948). *B. Leucosolenia botryoides* (Ellis and Solander). Section through flagellated epithelium of amphiblastula larva showing structure of "cellule en croix." (After Doboscq and Tuzet, 1942.) *C. Sycon coronatum* (Ellis and Solander). Section through "cellule en croix" of amphiblastula larva. Compare position of chromatic corpuscles with those of *Leucosolenia* and *Sycon raphanus*. (After Duboscq and Tuzet, 1941.) *D. Sycon raphanus* Schmidt. Sections through "cellules en croix" of amphiblastula larva in two views. (After Duboscq and Tuzet, 1937.) *a*. Siderophilic granules; *b*. flagellated cell; *c*. parabasal body; *d*. rows of chromatic corpuscles (Feulgen-negative); *e*. centroblepharoplast with fibrillar cone; *f*. nucleus; *g*. basal row of melanin granules; *h*. hyaline distal part of cell; *i*. fibrils connecting the crown of chromatic corpuscles to the cell membrane.

out that very few species of asconoid Calcarea have been studied with reference to the mode of origin of the flagellum of the choanocyte, the structure of the larva, or the direction of the crystalline optic axis in relation to the facial plane of the spicule, and commented that "if it were necessary to investigate these very obscure characters in every case, the classification of the group would indeed make slow progress." This is a cogent argument for the museum zoologist who is faced with the necessity of working up large collections of animals within a reasonable length of time. The use of these characters is all the more forbidding when it is realized that at least 111 species have been described in the genus *Leucosolenia*[6] alone (Tanita, 1943, who did

[6] Sarà's (1953) attempts to reduce the number of species in the genera *Clathrina* and *Leucosolenia* by relegating many species to "formae" because of overlap in skeletal characteristics seems unwarranted on embryologi-

not separate *Clathrina* from *Leucosolenia*). Furthermore, as Dendy and Row have remarked, specimens sent to taxonomists for determination are often not preserved in a state suitable for careful histological work, and larvae are rarely met with in specimens collected at random.

Some further criticisms of Bidder's classification given by Dendy and Row follow. (1) The occurrence in *Clathrina reticulum* (Schmidt) of a larval type transitional between parenchymula and amphiblastula (see Michin, 1900). In most species of *Clathrina* in which the development has been studied (e.g., *C. blanca, contorta,* and *coriacea*) the early larvae are blastulae with an epithelium which is uniformly flagellated except for one to four or more cells at the posterior pole (Fig. 4*C-I*). These posterior cells are non-flagellated and granular, and their fate as ectomesenchymal cells is already determined. As development proceeds, cells from the peripheral flagellated epithelium wander into the blastocoele from all points except the extreme anterior pole. The inwandering cells have lost their flagella and are presumptive ectomesenchymal cells. At the conclusion of this process the larva has become a compact, planula-like organism made up of three kinds of cells: peripheral flagellated cells, destined to become choanocytes; an inner mass of ectomesenchymal cells; and the still unchanged posterior granular cells (Fig. 4*C-II*). Such larve resemble the parenchymulae of some sponges of the class Demospongiae.

The larvae of *Clathrina reticulum* differ from the above account in lacking posterior granular cells (Fig. 4*B-I*) and in the fact that the ectomesenchymal cells arise through inwandering at the posterior pole only (Fig. 4*B-II*). This process of unipolar ingression recalls the condition seen in typical amphiblastula larvae in which, however, the peripheral epithelium is always sharply differentiated into an anterior flagellated region and a posterior non-flagellated region (Fig. 4*A-I*). In *Leucosolenia,* however, the non-flagellated region may be comparatively small at the time of release of the larvae but increases continually at the expense of the flagellated region during subsequent development. The late free-swimming larval stage of *Clathrina reticulum* thus approaches the early larva of *Leucosolenia* in form, so that the chief differences between these two species concern the timing of the developmental processes. Brien (1943) has noted that "the embryonic development of *Clathrina* is the most extended which exists among the sponges." The early blastula larva assumes what Brien calls a "pre-amphiblastula" stage and then, omitting the typical amphiblastula stage, develops into a parenchymula-like larva through multipolar or unipolar ingression.

Thus, although it is highly probable on embryological grounds that *Clathrina* and *Leucosolenia* are related phylogenetically, the observed differences between the larvae of the two genera seem sufficiently great to support Bidder's proposal for classifying the recent asconoid Calcarea. Reference may also be made to other characters distinguishing the two genera, such as the position of the flagellum relative to the nucleus of the choanocyte. Indeed it is the very fact of being based on a complex of characters which renders Bidder's classification useful.

Furthermore, it should be mentioned that the process of gastrulation differs in the two groups. Gastrulation in *Clathrina* is accomplished after the larvae have settled, at which time the peripheral endoblastic cells migrate through the ectomesenchyme to take up their position as the cells lining the spongocoele (Fig. 4*B-III*). Gastrulation in the case of the

cal grounds. Tuzet (1948), e.g., points out differences between the larvae of several species of *Clathrina: contorta* has four posterior granular cells, *blanca* has two such cells, *coriacea* has one, and *cerebrum* and *reticulum* lack these cells altogether. Minchin (1900) has noted, however, that all these variations in the posterior granular cells may occur as abnormalities in *C. blanca.*

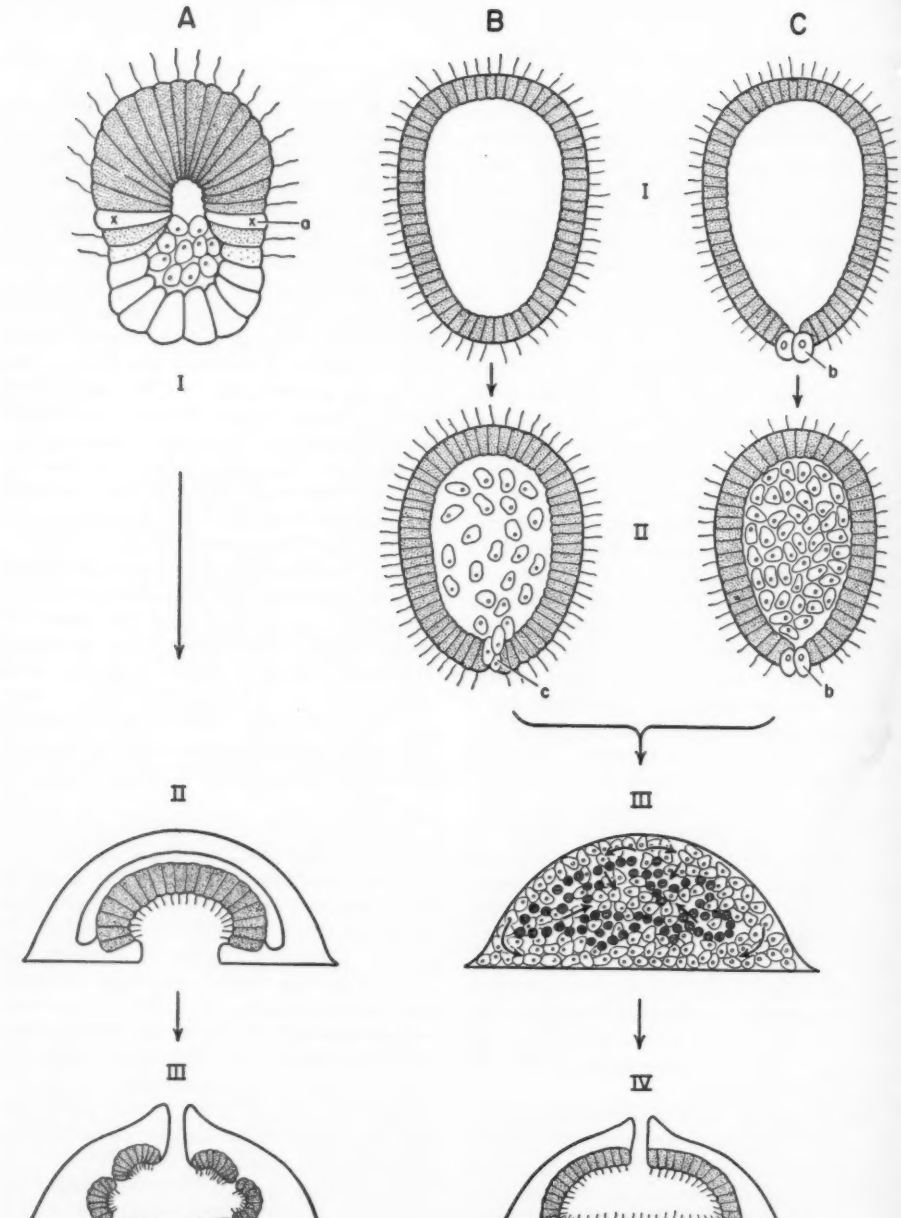

FIG. 4. Larval structure and metamorphosis in the Calcarea. *A*. Developmental stages typical of *Leucosolenia, Sycon, Grantia,* and related genera. I. Amphiblastula larva (late larva of *Leucosolenia* or newly released larva of *Sycon*). II. Newly settled larva showing gastrulation by invagination of the flagellated hemisphere. III. Young *Sycon* with osculum and beginning of formation of flagellated chambers. *B*. Developmental stages of *Clathrina reticulum* (Schmidt). I. Blastular larva. II. Parenchymula-like larva, showing unipolar ingression of ectomesenchymal cells. *C*. Developmental stages of *Clathrina blanca* (Miklucho-Maclay). I. Blastular larva. II. Parenchymula-like larva which has arisen through multipolar ingression. *B*. and *C*. III. Early settled larva showing gastrulation. IV. Young ascon-grade sponge with osculum and choanocytes lining spongocoele. a. "Cellule en croix"; b. posterior granular cells; c. region of ingression. (Modified from Brien, 1943, and Minchin, 1900).

amphiblastulae of *Leucosolenia, Sycon,* and related forms, involves invagination of the anterior hemisphere of flagellated cells which become the choanocytes lining the spongocoele and flagellated chambers (Fig. 4*A-II*).

(2) The supposition that both types of relationship between flagellum and nucleus in the choanocyte may occur in one genus (*Leucosolenia*) because Minchin (1909), following Goldschmidt (1907), reports such an occurrence within the protozoan genus *Mastigina.* Minchin's comments were in error, however, and were corrected in a later paper (Robertson and Minchin, 1910). In reality, Goldschmidt assigned his two new species of flagellates to different genera, in part *because of* the relation of the flagellum to the nucleus. Thus *vitrea,* with the flagellum arising independently of the nucleus, was placed in the genus *Mastigella; setosa,* with the flagellum arising from the nuclear membrane, was assigned to the genus *Mastigina.* Thus the two genera of flagellates in question are separated on the basis of characteristics identical with those used by Minchin to distinguish between *Clathrina* and *Leucosolenia.*

Hammer (1908) found that the nuclei of the choanocytes of *Sycon raphanus* Schmidt vary greatly in position, and this author criticized Minchin's phylogenetic conclusions based on nuclear position. Minchin (1909) answered this objection by pointing out that the significant fact is the relationship of the flagellum to the nucleus in the mature choanocyte. He stated further that in the larvae of both *Clathrina* and *Leucosolenia* the flagella are in direct contact with the nuclei (Fig. 2*C*). *Leucosolenia* and other Calcaronea may be regarded as neotenic in respect to this character. It is of interest to note also that Minchin (*op. cit.;* see also Robertson and Minchin, 1910) showed that when a clathrinid choanocyte divides, the nucleus moves to an apical position which it retains in the young cells which result (Fig. 5). As the daughter cells increase in size the nuclei move to their characteristic basal position. Bidder (1920*b*) has pointed out that food particles and fecal masses may temporarily displace the nucleus from its usual position. He stated that Hammer's Figure 85 "shows such a nucleus, with the agglomeration of ingested foreign bodies which have forced it down."

Hentschel (1923) retained the subdivisions Homocoela and Heterocoela for the Calcarea which he treated as an order of the phylum and class Porifera. In the Homocoela he placed the family Leucosoleniidae alone, recognizing both *Leucosolenia* and *Clathrina,* as well as *Ascute, Ascyssa,* and *Dendya.* He divided the Heterocoela as follows:

Series: Basinucleata	*Series: Apinucleata*
Family Leucascidae	Family Sycettidae
Family Leucaltidae	Family Heteropiidae
Family Lithonidae	Family Grantiidae
(= Minchinellidae)	Family Amphoriscidae
Family Murrayonidae	Family Dialytidae
	(= Lelapiidae)

Hentschel's classification, which combines the basic features of the opposing systems of Poléjaeff and Bidder, seems at first sight to be an acceptable alternative to the classification proposed by Bidder. However, by uniting the two lines of asconoid sponges in the same family, Hentschel has stressed the single character of grade of construction of the canal system and has ignored the array of characters listed earlier which separate the two groups and serve to unite them with the two heterocoelous series, the Basinucleata and the Apinucleata. Bidder's system, in which each of the two homocoelous lines is joined with the group of heterocoelous forms to which it has given rise, seems preferable to me since it is based upon a constellation of characters.

The names used by Hentschel for his family series under the Heterocoela were originally suggested by Bidder (1898) who speculated that eventually it might be possible to arrange all sponges (exclusive of the Hexactinellida) into two classes, the Basinucleata and Apinucleata, depending upon the position of the nu-

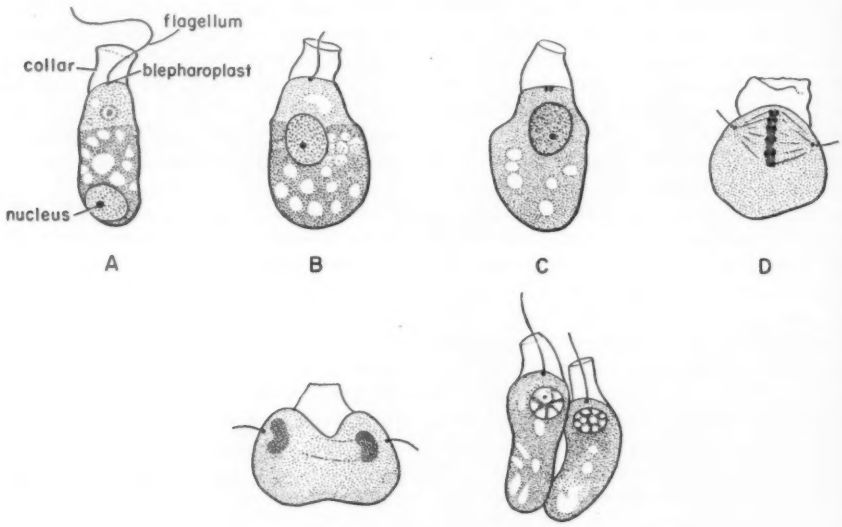

FIG. 5. Division of choanocyte in *Clathrina coriacea* (Montagu). *A*. Choanocyte during interphase with basal nucleus. *B*. Nucleus moving to apical position preparatory to mitosis. *C*. Choanocyte immediately before prophase. Nucleus apical; blepharoplast divided; flagellum lost. *D*. Late metaphase, showing new flagella arising from blepharoplasts which are still in close association with the centrosomes. *E*. Telophase. *F*. Young daughter cells; nuclei still apical in position. (After Robertson and Minchin, 1910.)

cleus in the choanocyte and the nucleus-flagellum relationship.

De Laubenfels (1936), like Bidder and Dendy and Row before him, rejected the names Homocoela and Heterocoela and followed the principles set forth by his predecessors in subdividing the class Calcarea. He was apparently unaware of Bidder's work, however, and proposed two new ordinal names, Asconosa and Syconosa. In the Asconosa, de Laubenfels included calcareous sponges which "appear to have passed almost directly from the ascon to the complicated leucon type"; in the Syconosa, on the other hand, he placed those calcareous sponges with a "considerable emphasis on the sycon type of architecture; very many of the genera have only this form, and the others give pronounced indications that they have passed through it in their attainment of a final leucon structure."

But De Laubenfels' names are used for artificial groups set up "merely for convenience" and lose their significance if a more nearly natural classification is followed. De Laubenfels found it difficult to place those species of the family Leucosoleniidae with choanocytes having the flagellum attached to an apical nucleus. He hinted that these species might be placed in the Order Syconosa (as the family Leucosoleniidae), leaving asconoid sponges with basal nuclei for grouping in the family Clathrinidae within the Asconosa. This action, involving a distribution of "ascon grade" sponges between the Asconosa and Syconosa, removes the significance of his original names and sets up a system identical with that of Bidder. But unless this action is taken, De Laubenfels' definitions of the orders Asconosa and Syconosa remain artificial and belie his statement "that it is preferable to use bases of separation that do have phylogenetic significance whenever such can be

discovered." De Laubenfels' statement that Dendy and Row have shown "that many of the Leucosoleniidae are intermediate in all respects and cannot possibly be sharply classified" is certainly an exaggeration of the arguments presented by these authors who concluded that it is quite likely that Bidder's classification "will ultimately prove to be thoroughly sound."

If it is indeed the aim of taxonomists to reflect phylogenetic trends in their work, the subdivision of the Calcarea into either Homocoela and Heterocoela or Asconosa and Syconosa is unacceptable. Adoption of Bidder's more natural separation of the Calcarea into Calcaronea and Calcinea [7] would serve a useful purpose in alerting taxonomists to the importance of the complex of characters supporting this system. In this way each worker might add such information as is feasible from the material before him, and the general validity of Bidder's scheme can be tested.

The perennial problem remains of where to place species of *Leucosolenia* for which data on nucleus-flagellum relations and embryology are not available. In his emendations of the generic diagnoses for *Clathrina* and *Leucosolenia*, Minchin (1896) stressed differences in colony form (Fig. 6) and the characteristics of the triradiate spicules (Fig. 1). "The full-grown *[Clathrina]* colony forms a system or systems of reticulate and anastomosing tubes, each system terminating in a cloaca-like osculum; incrusting, massive, or stalked. The principal spicules of the skeleton are equiangular triradiate systems, to which may be added sagittal triradiates in certain parts of the sponge, and monaxons." "The adult *[Leucosolenia]* colony has the form of a cluster of relatively large erect oscular tubes, which send out numerous diverticula and are often arborescent, united typically by a more or less stolon-like system of finer tubes. Triradiate systems always sagittal." Subsequent authors (Dendy and Row, 1913; Brøndsted, 1928; Sarà, 1953) have pointed out that the external form of asconoid sponges is too variable to serve as a reliable character for differentiating these two genera. Minchin emphasized that his characterizations of the form of colonies refer to *adult* individuals; it seems probable that some of the uncertainty expressed by subsequent authors arises from an attempt to apply the descriptions to immature colonies. Thus young specimens of *Clathrina* often have a simple olynthoid form (see *e. g.*, Sarà, 1953, Pl. 1, Fig. 1) and may be confused with *Leucosolenia*. The use of external form to identify isolated museum specimens of asconoid calcareous sponges is often impossible; but when populations of sponges are studied, it seems likely that the typical adult forms will be of some use as a first step in differentiating between the genera *Clathrina* and *Leucosolenia*.

In regard to spicule form as a means of distinguishing between the two genera, Tables 1 and 2 have been prepared to examine the correlation of this character with the position of the nucleus in the choanocyte and (or) the type of larva produced. All species of *Clathrina* and *Leucosolenia* for which I have found information concerning the last-mentioned two characters have been listed with their spicule characteristics. It is apparent that Minchin's use of the form of triradiate spicules is generally valid in separating *Clathrina* from *Leucosolenia*. Species of *Clathrina* have regular, equiangular triradiates exclusively or predominantly; species of *Leucosolenia* have sagittal, inequiangular triradiates exclusively or in part. Exceptions do occur, however. *Clathrina blanca* has a basic spiculation of sagittal, equiangular triradiates; usually some regular, equiangular ones occur as well. *C. pulcherrima* possesses some sagittal, inequiangular triradiates along with a predominance of regular, equiangular ones. On the other hand, *Leucosolenia eleanor* has a few regular, equiangular triradiates, although sagittal types predominate.

[7] Lameere (1937) is one of the few authors who have used Bidder's classification.

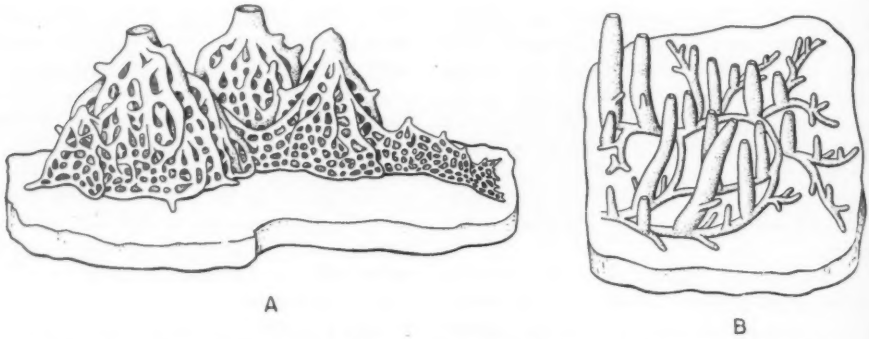

FIG. 6. *A* Mature colony of *Clathrina clathrus* (Schmidt). *B*. Mature colony of *Leucosolenia botryoides* (Ellis and Solander). (After Minchin, 1900.)

It seems to me that the question of assigning a given species to *Clathrina* or *Leucosolenia*, in the absence of cytological and embryological data, is not nearly as difficult as some authors have asserted. The characteristics of the triradiate spicules will give a satisfactory answer in most cases. Problematical species such as *blanca* (in which sagittal, equiangular triradiates predominate in spite of clathrinid affinities) and *stolonifer* (in which triradiates are absent) can be placed with certainty only after a study of the choanocytes and larvae, to be sure. Where such data are wanting, species can only be placed in one genus or the other in accordance with the best judgment of the author describing them. Tables 1 and 2 should prove helpful in many cases in evaluating the spicule characteristics and in placing species in one of the two genera.

Bidder's subdivision of the subclasses Calcaronea and Calcinea into orders may be questioned. Within the Calcaronea he proposed the order Asconida for the family Leucosoleniidae and the order Sycettida for the families Sycettidae, Grantiidae, Heteropidae, and Amphoriscidae. The name Asconida seems inappropriate since asconoid sponges are divided between both subclasses in his classification. It is proposed to substitute the name Leucosoleniida for this order. Bidder's order Sycettida includes the vast majority of recent calcareous sponges which appear to form a natural assemblage. The family Lelapiidae, a pharetronoid group, shows some relationship to the Grantiidae according to Dendy and Row and should be included here. It is perhaps unfortunate that the name Sycettida was chosen rather than Syconida after the most typical and best-known genus of the group.

Bidder divided the Calcinea into the orders Ascettida (to include the families Clathrinidae and Leucascidae) and Ascaltida (to include his families Reticulatae and Heteropegmidae). His choice of these names is regrettable since both *Ascetta* Haeckel and *Ascaltis* Haeckel have fallen in synonymy in recent usage. The family Reticulatae, in which Bidder placed the genera *Ascaltis* and *Ascandra*, may be included within the Clathrinidae; and the genus *Dendya* Bidder, which he had placed in the family Heteropegmidae, is also a clathrinid. *Heteropegma* Polejaeff is a synonym of *Leucaltis* and the family name Leucaltidae as redefined by Dendy and Row (1913) should be adopted to include the genera *Leucaltis* Haeckel *emend.* Dendy and Row and *Leucettusa* Haeckel *emend.* Dendy and Row.

A more natural arrangement of the Calcinea would result from placing the Clathrinidae in a new order, the Clathrinida, and including the families Leucascidae

TABLE 1—SPICULE CHARACTERISTICS OF SPECIES OF CLATHRINA

SPECIES	LARVAL TYPE	POSITION OF NUCLEI IN CHOANOCYTES	MONAXONS	TRIRADIATES	QUADRIRADIATES	CHARACTERISTICS OF TRIRADIATES
blanca (Miklucho-Maclay, 1868)	Parenchymula	?		x		Mostly sagittal, equiangular. A few regular, equiangular.
cavata (Carter, 1886)	?	Basal	x	x	x	Regular, equiangular.
cerebrum (Haeckel, 1872)	Parenchymula	?		x	x	Mostly regular, equiangular. Contorted forms at surface.
clathrus (Schmidt, 1864)	Parenchymula	?		x		Mostly regular, equiangular. Basal ray may be slightly longer.
contorta (Bowerbank, 1866)	Parenchymula	?	x	x	x	Regular, equiangular.
coriacea (Montagu, 1818)	Parenchymula	Basal		x	x	Mostly regular, equiangular. Basal ray may be slightly longer.
depressa (Dendy, 1891)	?	Basal	x		x	Regular, equiangular.
falcata (Haeckel, 1872)	?	Basal	x	x	x	Regular, equiangular.
gardineri (Dendy, 1913)	?	Basal		x	x	Regular, equiangular.
pelliculata (Dendy, 1891)	?	Basal	x	x	x	Mostly regular, equiangular. A few sagittal, equiangular.
proxima (Dendy, 1891)	?	Basal		x		Regular, equiangular.
pulcherrima (Dendy, 1891)	?	Basal		x		Regular, equiangular to sagittal, inequiangular.
reticulum (Schmidt, 1862)	Parenchymula	?	x	x	x	Regular, equiangular. Angles may be subequal.
stolonifer (Dendy, 1891)	?	Basal	x		x	Absent
ventricosa (Carter, 1886)	?	Basal	x	x	x	Regular, equiangular.
vitrea (Row and Hôzawa, 1931)	?	Basal		x	x	Regular, equiangular.

and Leucaltidae in a new order, the Leucettida. The latter order is named for the genus *Leucetta* Haeckel, 1872, *emend.* Dendy and Row, 1913, the most widely distributed genus. The families Minchinellidae and Murrayonidae may be placed in the order Pharetronida. Most of the fossil pharetronid sponges would be included in this order, although it is probable that some are more nearly related to the family Lelapiidae (*fide* Dendy and Row, *op cit.*).

TABLE 2—SPICULE CHARACTERISTICS OF SPECIES OF LEUCOSOLENIA

SPECIES	LARVAL TYPE	POSITION OF NUCLEI IN CHOANOCYTES	MONAXONS	TRIRADIATES	QUADRIRADIATES	CHARACTERISTICS OF TRIRADIATES
botryoides (Ellis & Solander, 1786) [= *variabilis* (Haeckel, 1872)]	Amphiblastula	Apical	x	x	x	Sagittal, mostly inequiangular.
complicata (Montagu, 1818)	?	Apical	x	x	x	Sagittal, inequiangular.
eleanor Urban, 1906	?	Apical	x	x	x	Usually sagittal, equiangular or inequiangular; some regular, equiangular; some irregular.
lucasi Dendy, 1891	?	Apical	x	x	x	Sagittal, almost equiangular.

The classification [8] of the Calcarea proposed here may be outlined as follows:

SUBCLASS CALCINEA Bidder, 1898. Diagnosis: Nucleus of choanocytes basal, the flagellum arising independently of the nucleus. Parenchymula-like larvae produced. At least some of the triradiates (when present) equiradiate and equiangular in most cases. Monaxons present (seldom lance-headed) or absent. Triradiates the first spicules to appear in the newly settled sponge.

ORDER CLATHRINIDA *Ordo Nov.* Diagnosis: Spongocoele lined with choanocytes throughout life. No true dermal membrane or cortex developed.

Family Clathrinidae Minchin, 1900, *emend.* 1909. (Genera *Clathrina, Ascute, Dendya*).

ORDER LEUCETTIDA *Ordo Nov.* Diagnosis: Grade of construction of the canal system syconoid to leuconoid. Spongocoele not lined with choanocytes; these cells restricted to flagellated chambers. Distinct dermal membrane or cortex present.

Family Leucascidae Dendy, 1892, *emend.* Dendy and Row, 1913.

Family Leucaltidae Dendy and Row, 1913.

ORDER PHARETRONIDA Zittel, 1878, *emend.* Diagnosis: Canal system leuconoid. Main skeleton composed of quadriradiates joined together by a calcareous cement or comprising a rigid calcareous network not composed of spicules.

Family Minchinellidae [9] Dendy and Row, 1913.

Family Murrayonidae [9] Dendy and Row, 1913.

SUBCLASS CALCARONEA Bidder, 1898. Diagnosis: Nucleus of choanocytes apical, the flagellum arising directly from the nucleus. Amphiblastula larvae produced. Triradiates predominantly sagittal. Monaxons (often lance-headed) usually present. Monaxons the first spicules to appear in the newly settled sponge.

ORDER LEUCOSOLENIIDA *Ordo Nov.* Diagnosis: Spongocoele lined with choanocytes throughout life. No true dermal membrane or cortex developed.

Family Leucosoleniidae Minchin, 1900, *emend.* 1909. (Genera *Leucosolenia* and *Ascyssa*).

ORDER SYCETTIDA Bidder, 1898.

[8] The arrangement of genera in families follows that of Dendy and Row (1913) except for the families of Clathrinidae and Leucosoleniidae for which new arrangements are indicated.

[9] De Laubenfels (1936) united these families to form the family Petrostomidae, but it seems to me that Dendy and Row have given ample evidence for recognizing them as distinct.

Diagnosis: Grade of construction of canal system syconoid to leuconoid. Spongocoele not lined with choanocytes; these cells restricted to flagellated chambers. Distinct and continuous dermal membrane or cortex absent in the Sycettidae, but present in the remaining families.

Family Sycettidae Dendy, 1892.

Family Heteropiidae [10] Dendy, 1892.

Family Grantiidae Dendy, 1892, *emend.* Dendy and Row, 1913.

Family Amphoriscidae Dendy, 1892, *emend.* Dendy and Row, 1913.

Family Lelapiidae Dendy and Row, 1913.

REFERENCES CITED

BIDDER, G. P. 1898. The skeleton and classification of calcareous sponges. *Proc. Roy. Soc. London 64*:61–76.

——— 1920*a*. The fragrance of calcinean sponges and the spermatozoa of *Guancha* and *Sycon*. *J. Linn. Soc.* (*Zool.*), *34*:299–304.

——— 1920*b*. Notes on the physiology of sponges. Note G. Migration of the nucleus in collar-cells. *J. Linn. Soc.* (*Zool.*), *34*: 324–325.

BOWERBANK, J. S. 1866. A monograph of the British Spongiadae. Vol. 2, 388 p. London, Ray Soc.

BRIEN, PAUL. 1943. L'embryologie des éponges. *Bull. Mus. Hist. Nat. Belgique, 19*(16):20 p.

BRØNDSTED, H. V. 1928. Die Kalkschwämme der deutschen Südpolar-Expedition 1901–1903. *Dtsch. Südpol. Exped., 20*:1–47.

CARTER, H. J. 1886. Descriptions of sponges from the neighbourhood of Port Phillip Heads, South Australia, continued. *Ann. Mag. Nat. Hist.*, (5) *17*:502–516.

DE LAUBENFELS, M. W. 1936. A discussion of the sponge fauna of the Dry Tortugas in particular and the West Indies in general, with material for a revision of the families and orders of the Porifera. *Publ. Carnegie Instn., 467*:225 p. (*Pap. Tortugas Lab., 30*).

DENDY, ARTHUR. 1891. A monograph of the Victorian sponges. Part I. The organization and classification of the Calcarea Homocoela, with descriptions of the Victorian species. *Trans. Roy. Soc. Victoria, 3*(1):1–81.

——— 1892. Synopsis of the Australian Calcarea Heterocoela; with a proposed classification of the group and descriptions of some new genera and species. *Proc. Roy. Soc. Victoria, 1892*:69–116.

——— 1913. Report on the calcareous sponges collected by H. M. S. "Sealark" in the Indian Ocean. *Trans. Linn. Soc. London* (*Zool.*), (2)*16*:1–29.

DENDY, ARTHUR and Row, R. W. H. 1913. The classification and phylogeny of the calcareous sponges, with a reference list of all the described species, systematically arranged. *Proc. Zool. Soc. London*, 704–813.

DUBOSCQ, O. and TUZET, O. 1937. L'ovogenèse, la fécondation, et les premiers stades due développement des éponges calcaires. *Arch. Zool. Exp. Gén., 79*:157–316.

——— 1941. Sur les cellules en croix des *Sycon* (*Sycon ciliatum* Fabr., *Sycon coronatum* Ellis et Sol., *Sycon elegans* Bower.) et leur signification. *Arch. Zool. Exp. Gén., 81*: Notes et revue (4), 151–163.

——— 1942. Recherches complémentaires sur l'ovogenèse, la fécondation, et les premiers stades du développement des éponges calcaires. *Arch. Zool. Exp. Gén., 81*:395–466.

ELLIS, JOHN. 1786. The natural history of many curious and uncommon zoophytes, collected from various parts of the globe. (Edited by Daniel Solander). London, Benj. White and Son, 206 p.

GOLDSCHMIDT, RICHARD. 1907. Lebensgeschichte der Mastigamöben *Mastigella vitrea* n. sp. und *Mastigina setosa* n. sp. *Arch. Protistenk.*, Suppl. *1*:83–168.

HAECKEL, ERNST. 1872. Die Kalkschwämme. Vol. 2, 418 p.; vol. 3, 60 Pl. Berlin, Georg Reimer.

HAMMER, ERNST. 1908. Neue Beiträge zur Kenntnis der Histologie und Entwicklung von *Sycon raphanus*. *Arch. Biontol., 2*:291–334.

HENTSCHEL, ERNST. 1923. Porifera. (*in:* Kükenthal, Willy, *Handbuch der Zoologie, 1*: 307–418.) Berlin, Walter de Gruyter and Co.

HERLANT-MEEWIS, HENRIETTE. 1949. Contribution à l'étude histologique des Spongiaires. *Ann. Soc. Zool. Belgique*, 1948, *79*:5–36.

JONES, W. C. 1954. Spicule form in *Leucosolenia complicata*. *Quart. J. Micr. Sci., 95*(2): 191–203.

——— 1956. Colloidal properties of the mesogloea in species of *Leucosolenia*. *Quart. J. Micr. Sci., 97*(2):269–285.

LAMEERE, AUGUSTE. 1932. Précis de Zoologie. Tome I. (Deuxième Ed.) *Publ. Inst. Zool. Torley-Rousseau*. 394 p.

LÉVI, CLAUDE. 1953. Sur une nouvelle classifi-

[10] De Laubenfels (1936) changed the name of this family to Djeddeidae because *Djeddea* Haeckel antedates the generic name *Heteropia* Carter. Later he suggested dropping Djeddeidae and using Heteropiidae (*in litt.*, 1950).

cation des Démosponges. *C. R. Acad. Sci. Paris, 236*:853–855.

——— 1956. Étude des *Halisarca* de Roscoff. Embryologie et systématique des Démosponges. *Arch. Zool. Exp. Gén., 93*(1):1–181.

——— 1957. Ontogeny and systematics in sponges. *Syst. Zool., 6*(4):174–183.

MIKLUCHO-MACLAY, N. 1868. Beiträge zur Kenntniss der Spongien. *Jena. Z. Naturw., 4*: 221–240.

MINCHIN, E. A. 1896. Suggestions for a natural classification of the Asconidae. *Ann. Mag. Nat. Hist.*, (6)*18*:349–362.

——— 1900. Sponges. (*in*: Lankester, E. R., *A treatise on zoology*, part 2, 178 p.) London, Adam and Charles Black.

——— 1909. The relation of the flagellum to the nucleus in the collar-cells of calcareous sponges. *Zool. Anz., 35*(8):227–231.

MONTAGU, GEORGE. 1818. An essay on sponges, with descriptions of all species that have been discovered on the coast of Great Britain. *Mem. Wernerian Nat. Hist. Soc.*, Edinburgh, *2*:67–122.

POLÉJAEFF, N. 1883. Report on the Calcarea dredged by H. M. S. Challenger during the years 1873–76. *Rept. Scient. Results Voy. Challenger, 24*:76 p.

ROBERTSON, MURIEL and MINCHIN, E. A. 1910. The division of the collar-cells of *Clathrina coriacea* (Montagu): a contribution to the theory of the centrosome and blepharoplast. *Quar. J. Micr. Sci.*, (2)*55*:611–640.

ROW, R. W. H. and HÔZAWA, SANJI. 1931. Report on the Calcarea obtained by the Hamburg South-West Australian Expedition of 1905. *Sci. Rept. Tohôku Univ.*, (4) *6*(4): 727–809.

SARÀ, MICHELE. 1953. Variabilità delle Leucosolenie del Golfo di Napoli e nuove vedute sulla sistematica del gruppo. *Annu. Ist. Zool. Univ. Napoli, 5*(7):110 p.

SCHMIDT, OSCAR. 1862. Die Spongien des adriatischen Meeres. 88 p., Leipzig, Wilhelm Engelmann.

——— 1864. Supplement der Spongien des adriatischen Meeres enthaltend die Histiologie und systematische Ergänzungen. 48 p., Leipzig, Wilhelm Engelmann.

TANITA, SENJI. 1943. Key to all the described species of the genus *Leucosolenia* and their distribution. *Sci. Rept. Tohôku Univ.*, (4) *17*(1):71–93.

TUZET, ODETTE. 1948. Les premiers stades du développement de *Leucosolenia botryoides* Ellis et Solander et de *Clathrina* (*Leucosolenia*) *coriacea* Mont. *Ann. Sci. Nat. Zool.*, (11) *10*:103–114.

URBAN, FERDINAND. 1906. Kalifornische Kalkschwämme. *Arch. Naturgesch., 72*(1):33–76.

ZITTEL, K. A. 1878. Studien über fossile Spongien. Dritte Abtheilung: Monactinellidae, Tetractinellidae und Calcispongiae. *Abh. Bayer. Akad. Wiss., 13*(2):48 p.

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What *is* the Subspecies Problem?

ANDREW STARRETT

SINCE 1953, when the now-famous paper by Wilson and Brown appeared in this journal, there has been a renewed controversy raging over what is often called the "subspecies problem." No less than 19 papers dealing directly with this question have been published in *Systematic Zoology* since that paper came out, along with six others which have contained expressed or tacit comments on the problem. The extremes of viewpoint have varied from that expressed by Gosline (1954), Burt (1954), and Doutt (1955), among others, namely that the subspecies concept should be discarded along with the legality of the trinomial (the viewpoint championed by Wilson and Brown, *op. cit.*), to that of Mayr (1954), Parkes (1955), Fox (1955), and Durrant (1955) which calls for the retention of the present taxonomic status of the subspecies. Almost to a man, however, these authors expressed discontent with the present situation in zoological taxonomy as regards the sometimes unwise use of the subspecies concept and the indiscriminate naming of infraspecific populations. Actually, a cline of opinion is presented from a "leave the subspecies concept and usage as flexible and indefinite as they now are" viewpoint, through varying degrees of thoroughness in attempting to define more clearly the concept, to the other extreme as proposed by Wilson and Brown. Many of those on both sides of the issue proposed changes in the present system with the intention of improving the situation. These new proposals vary from the substitution of symbols (Burt, *op. cit.*) or a "simple vernacular locality citation or a brief statement of the range involved" (Wilson and Brown, *op.cit.*) for the trinomen, to a more concisely defined subspecies category (Edwards, 1954) which would be less subjective in its application. By implication, if not by direct statement, most authors have laid the blame for the somewhat chaotic present day situation on the less responsible, less discriminating and, perhaps, less concerned taxonomists of the present and immediate past. That the unwise use of the subspecies concept and its concomitant nomenclatorial privileges has been to some extent responsible for the present situation cannot be denied. However, this is certainly not the entire picture, as I will point out presently.

Classification in biology, as in any other science, is merely a reflection of the basic human desire (or need) to categorize. People must identify and classify things in order to think about them or communicate with one another concerning them. In a field of science in which the objects of study may have a prohibitively large and confusing number of common names, such as is the case in biology, it becomes necessary to provide, for the sake of accuracy, a system which contains a minimum of ambiguity.

Early classification systems were almost necessarily basically typological for a number of reasons. Collections were often rather provincial in scope, "exotic" specimens being poorly represented in numbers and kinds; biologists had to do without the more recent genetic concepts and evolutionary theories which have been vitally important to recent systematic progress. One has only to compare the classifications of Aristotle, Linnaeus, and the modern specialists, in the light of present day knowledge, to see the changes which have taken place as more has become known about the biological world and its processes. However, during the early stages of the categorization of the organic world, many of the pioneer "taxonomists" had a natural desire to know

about the relationships of the animals and plants which they were classifying, and so they attempted to set up natural classifications on the basis of their limited knowledge. This aim of erecting a natural system of classification, i.e. one which reflects the phylogenetic relationships of living organisms, is still one of the taxonomic goals of the present time. Among other things, then, the modern zoological systematist is attempting not only to identify and name the animals with which he comes in contact, but also to place them in a classification which will indicate their natural affinities. In order to do this, more and more techniques have been, and are being, devised which will provide information about relationships (for instance, in biochemistry, physiology, experimental genetics), and larger series of specimens are being used for comparison and for studies of variation. As a consequence, our knowledge of some groups of animals is growing at an increasing rate. It is just this advancement in knowledge and techniques in the different animals groups which has been partially responsible for the problems that now face us. This was pointed out by Clark in his recent thought-provoking paper (1955). Our methods of analysis and our increasing knowledge are getting ahead of our system of classification. This is true of all categories, but it is particularly pressing at and below the level of the genus. One need only read such papers as those by James (1953) and Cain (1956) on the generic category, and Hubbs (1955) on hybridization in fishes, to see what the problems at this level are. Sylvester-Bradley (1954) and Cain (1955) have discussed the superspecies concept. Even more significant in relation to the present problem have been those papers dealing with the species: Meglitsch (1954) reviewed the species concepts which have been, and still are, in use, and provided a synthesized description of what he thought they should imply; Clark (*op.cit.*) reviewed the nature of the species and the taxonomic consequences of increased knowledge concerning the natural groupings which we call species; Ross (1956) compared the concepts of taxonomic holotype and biological species; and Rudd (1955) presented a concrete problem, concerning the use of the lower taxa, which arose as part of a study of several living populations. All four of these papers reflect the effects of increased knowledge and improved techniques on the field of systematics. They all point up the dynamic nature of natural populations of living organisms and the backwardness of the static, commonly accepted concept(s) of the species in taxonomy. Most taxonomists (or systematists) are biologists, and it is, therefore, increasingly difficult to contain the conclusions which have been derived from evidence concerning relationships in what is becoming an unrealistic system of classification, *if* true relationship is to be an important factor in this classification. This very conflict is felt most strongly at the infraspecific level, particularly in those groups which are being most thoroughly studied. Here, then, is one of the causes of the present upheaval and discontent which is taking the form of healthy controversy.

The species is generally thought of by the vast majority of biologists as the real, the basic, unit of systematics upon which our whole classification is built. Indeed, it would be considered by many to be pure heresy to consider another possibility (although Burma states that the "basic taxonomic unit" is the subspecies [1949]). Yet there has been no real agreement on a good inclusive definition of the concept. This is not to say that the general concept of the species is not valid, but that the extent of its objectivity depends upon the person who is employing the concept. Most biologists probably do not think a great deal about delimiting the idea of species in their own minds, although almost any one of them will tell you that he knows what a species is. There is undoubtedly a fairly general acceptance of one or another of the "standard" species

definitions with, perhaps, slight reservation concerning some point or other (see Mayr, 1942; Meglitsch, *op.cit.*, for summaries of the "standard" species definitions). Yet when one does begin to think at any length about the concept, he either has to make certain reservations or the result is a long definition with numerous qualifications (see further Nitecki, 1957, for the paleontological implications of the species concept). One simply cannot make a simple, all-inclusive definition of the species. How, then, can the subspecies concept be very objective if what is generally acknowledged to be the least subjective concept (as a taxonomic or biological unit) is a bit fuzzy around the edges? Those who do not feel at least a little distaste for this lack of objectivity at a taxonomic level so close to the biological units with which they are working (*i.e.*, the individual animals), are perhaps those who are least concerned with the questions being raised here, and are therefore satisfied with the system of classification as it now stands.

But, what has actually caused the recent renewed outbreak of controversy over the application of the subspecies concept? As I have already indicated, it was not entirely prompted by those who have been careless in their dealings with this taxon, since there were undoubtedly irresponsible taxonomists in the days before the use of the subspecies category became a problem. These individuals have merely lit the fuse at a time of proper conditions which, as I also mentioned above, have been brought about by our advanced state of knowledge and increased ability to determine relationships (see Hubbell, 1954). However, a large portion of the controversial element has been supplied by arguments, concerning the validity and usability of the subspecies concept, between workers in different groups which have not reached the same stage in evolution of systematics and which, therefore, present different problems at the lower taxonomic levels. In addition, the biologies of the animals represented by the various groups differ and the actual problems of relationships are often not comparable. Consider, for instance, what would happen if an ichthyologist were to attempt to revise a genus of protozoans! The basic systematic (biological!) problems in the two groups are so different that he would be forced to revise completely his taxonomic approach before entering into the undertaking (see, for example, Hubbs, *op.cit.*, and Corliss, 1956). This is perhaps an extreme example, but differences do exist between any two of the larger groups of animals you might wish to compare, even within some classes. Anyone who presents synthesized arguments on the problem at hand cannot but be biased by his own experiences with a particular group of animals, and for this reason it is often easy for another worker in a different group to find fault with some of the arguments presented.

I feel, then, that the most immediately useful discussions of the subspecies category are those by people concerned with the systematics of particular groups of animals. Such discussions (for instance, those by Fox, 1955, and Gillham, 1956, concerning Lepidoptera) bring up practical points which may be of benefit to other workers interested in the same group. In addition, discussions of this nature may provide ideas or information which is applicable to problems in other groups *if* the basic biological properties of both groups are kept in mind. Those who would concern themselves with the philosophical questions about the validity and usefulness of the subspecies concept would do well to consider the entire system of classification in the same light.

The use of infraspecific categories is not an innovation in systematics; they have been employed, in one form or another, for a good many years. At a certain stage in the evolution of the systematics of each group of animals they have served (or, in some groups, may yet serve) a purpose, and at that particular stage they were not considered objectionable by most sys-

tematists. Now that theoretical background, knowledge and systematic techniques have reached an advanced stage in some groups, systematists working in those groups are beginning to realize the shortcomings of the present system of classification, shortcomings which are emphasized by the problems arising at the specific and infraspecific levels.

The basic problem as I see it, then, comprises these questions:

(1) Is the present system of classification satisfactory in the light of what we are beginning to learn about relationships in various groups?

(2) If we are not satisfied with this system, can we provide another which would serve as a utilitarian classification and adequately show relationships at the same time? (see Simpson, 1945:12–14).

(3) If the present system is not satisfactory, and we are to be concerned with "true" relationships, are the present categories (including subspecies) still of value? This means that the species concept needs special scrutiny (see Burma, 1954).

(4) Would it be more desirable to devise a good working classification at the expense of a natural system? Admittedly, this is now the case in some of the higher categories (see Borgmeier, 1957).

(5) If our primary concern is to set up a purely utilitarian system of classification, whether the present one is acceptable or not, are the present categories useful? In this case, more restricted definitions of the lower categories would be necessary.

Whatever the answers to these questions may be, at present the decision concerning the application of the subspecies concept and its use in taxonomy should rest with the workers in each group of animals. Having made this decision, systematists will still be faced with the same basic considerations listed by Fox (*op. cit.*): "(1) the organisms under consideration must be analyzed biologically, (2) the organisms must be assigned to a taxonomic level, (3) the taxa must be named or not named in accordance with the International Rules." The decision should certainly not be influenced by what can be done by irresponsible taxonomists, since the elimination of the subspecies category on this basis would only result in the misuse of the species by these same people. Rather, it should be based upon careful consideration of the questions listed above, for these represent the heart of the problem. A universal decision on the subspecies question, without first deciding what are to be the aims of the system of classification, is impractical. Furthermore, a universal decision would not be realistic at present, since systematics has reached different stages of advancement in the various animal groups.

The question of the biological validity of the subspecies *concept* is important only if a natural phylogenetic classification is to be used, in which case any decision should influence strongly the use of the subspecies category in taxonomy. On the other hand, the significance of the subspecies *category* itself becomes the primary question if a purely utilitarian classification is deemed desirable. In addition, it should be remembered that the inclusion of the subspecies category in the nomenclatorial hierarchy no more demands its use in all groups of animals than would its exclusion demand the cessation of studies of infraspecific variation or of infraspecific populations.

Let me close this discussion with the admission that this may have been *largely a summary of the obvious*. However, after reading some of the recent papers on the "subspecies problem," I have become concerned about the possibility that many people probably are not aware, or not willing to admit, that a long-standing institution such as our present system of classification may be losing its usefulness, and that the somewhat heated controversy which is now in progress may be a reflection of this change. Perhaps the questions raised here will serve to stimu-

late more thought about the whole problem instead of just one phase of it.

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LITERATURE CITED

BORGMEIER, T. 1957. Basic questions of systematics. *Syst. Zool., 6*:53–69.

BURMA, B. H. 1949. The species concept: a semantic review. *Evol., 3*:369–370, 372–373.

——— 1954. Reality, existence, and classification: a discussion of the species problem. Madroño, *12*:193–209.

BURT, W. H. 1954. The subspecies categories in mammals. *Syst. Zool., 3*:99–104.

CAIN, A. J. 1955. Not the superspecies. *Syst. Zool., 4*:143–144, 139.

——— 1956. The genus in evolutionary taxonomy. *Syst. Zool., 5*:97–109.

CLARK, R. B. 1956. Species and systematics. *Syst. Zool., 5*:1–10.

CORLISS, J. O. 1956. Evolution and systematics of ciliates. *Syst. Zool., 5*:68–91; 121–140.

DOUTT, J. K. 1955. Terminology of microgeographic races in mammals. *Syst. Zool., 4*: 179–185.

DURRANT, S. D. 1955. In defense of the subspecies. *Syst. Zool., 4*:186–190.

EDWARDS, J. G. 1954. A new approach to infraspecific categories. *Syst. Zool., 3*:1–20.

FOX, R. M. 1955. On subspecies. *Syst. Zool., 4*:93–95.

GILLHAM, N. W. 1956. Geographic variation and the subspecies concept in butterflies. *Syst. Zool., 5*:110–120.

GOSLINE, W. A. 1954. Further thoughts on subspecies and trinomials. *Syst. Zool., 3*: 92–94.

HUBBELL, T. H. 1954. The naming of geographically variant populations. *Syst. Zool., 3*:113–121.

HUBBS, C. L. 1955. Hybridization between fish species in nature. *Syst. Zool., 4*:1–20.

JAMES, M. T. 1953. An objective aid in determining generic limits. *Syst. Zool., 2*:136–137.

MAYR, E. 1942. Systematics and the origin of species. Columbia Univ. Press, N. Y.

——— 1949. The species concept: semantics versus semantics. *Evol., 3*:371–372.

——— 1954. Notes on nomenclature and classification. *Syst. Zool., 3*:86–89.

MEGLITSCH, P. A. 1954. On the nature of species. *Syst. Zool., 3*:49–65.

NITECKI, M. H. 1957. What is a paleontological species? *Evol., 11*:378–380.

PARKES, K. C. 1955. Sympatry, allopatry, and the subspecies in birds. *Syst. Zool., 4*:35–39.

ROSS, E. H. 1956. What is species describing? *Syst. Zool., 5*:191–192.

RUDD, R. L. 1955. Population variation and hybridization in some California shrews. *Syst. Zool., 4*:21–34.

SIMPSON, G. G. 1945. The principles of classification and a classification of mammals. *Bull. Amer. Mus. Nat. Hist., 85.*

SYLVESTER-BRADLEY, P. C. 1954. The superspecies. *Syst. Zool., 3*:145–147.

WILSON, E. O. and BROWN, W. L., JR. 1953. The subspecies concept and its taxonomic application. *Syst. Zool., 2*:92–111.

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The Synthetic Natural Populational Species in Biology

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PERHAPS the most exasperating of all debates in biology centers upon the definition of the natural species. The main fruit of the debates has been the clarification that indeed there are numerous concepts of different sorts of collectives (for living organisms), any one of which might be or has been termed a species. But the problem of which concept biologists should agree is most deserving of the name species has not been settled, although there is some agreement upon what should *not* receive that name.

The symposium entitled *The species problem* recently published by the American Association for the Advancement of Science (Mayr, 1957) includes a series of papers presenting various points of view that may collectively be interpreted as setting the background for a synthetic view toward which modern thought may be trending in attainment of the state of general acceptability. In brief, this synthetic view is that (1) there are three entirely different populational hierarchies in the organic world, each requiring recognition of units for identification at several levels; (2) that the units of one system, regardless of name, are not at all homologous with those of the other systems; (3) that the names for the units already established for the most highly evolved and best known system, the Mendelian system, be utilized in all systems; and that (4) the criteria for those units in the Mendelian system be applied, as closely as possible, to the other systems.

Zoologists dealing with heterosexually reproducing animals have been impressed with the "biological" concept of species, the core of which is the existence of a separate common gene pool for each entity called a species; all individuals share in that gene pool, and are incapable of sharing in other gene pools. It is understood that each gene pool recognized as a species must be occupied by individuals always recognizably different from members sharing in other gene pools, even though the differences may be extremely difficult to test. Species differing solely in characters that tax the testing ability of students of their taxonomy are called *sibling* or *cryptic* species; those that differ in readily observable characters are here called *phaneric* species.

This term "biological species" is also used in another sense, namely in reference to biotypes, which may or may not actually be regarded as species. A preferable term for biological species, in the sense here intended, is the *Mendelian species*, which consists of Mendelian, therefore heterosexually reproducing, populations (see Dobzhansky, 1950, p. 401).

Zoologists dealing with asexually and unisexually reproducing animals, on the contrary, are not so impressed with the Mendelian concept. Sonneborn (in Mayr, 1957, p. 155) points out that, if this were to be accepted as the sole definition for species, over half of the species to be recognized on current standards would be invalid. If not species, what are they? Mayr (1957, p. 380) does not admit that the percentage of asexual and unisexual organisms is so overwhelming, but the problem would exist and could not be ignored even if only 15–25 per cent of all organisms were excluded from consideration as species at all.

Sonneborn further claims that restriction of the term species to the "biological" concept is unwise because of the practical impossibility of ever establishing the parameters or even existence of the gene

pool in more than a small per cent of heterosexually reproducing organisms. On the contrary, surely it is the thing in nature that is the species; our inability adequately to test the thing in nature does not invalidate it. Morphological and physiological data obviously can be interpreted in various ways; to fail to place them for interpretation on the framework of the Mendelian concept would be to revert to totally artificial criteria for the species.

Sonneborn points out, I think rightfully, that no limitation of the term species to one group of organisms, say those that reproduce heterosexually, is justifiable or even possible. The term species, in application to organisms, has always referred to units of identification of all types, not just one. This is a basic premise of his approach to the problem; it is basic to the present discussion, and I think is generally admitted. The entire following discussion is valid only if this premise is granted.

If the term species cannot be *restricted* to the gene pools of Mendelian populations (i.e., heterosexually reproducing populations), what is the solution? Sonneborn (*op. cit.*) suggests that taxonomists should revert to a "degree of difference" criterion for species, applicable to all organisms. By this system he would recognize two infrageneric populational categories, namely the *species* and *syngen*. Sonneborn's species is a group of organisms irreversibly divergent from other groups and possessing readily visible discontinuities from other groups. This definition actually describes our familiar phaneric species but interpreted as occurring in all organisms irrespective of mode of reproduction. Cryptic Mendelian species are not, by Sonneborn's definition, really species at all. For them and for the analogous, slightly differentiated but genetically irreversible clones, host types and biotypes so abundant in asexually and unisexually reproducing organisms he suggests the term *syngen*, which would of course not be eligible for scientific names. "A syngen, like a species, has thus passed the threshold of irreversible evolutionary divergence; but unlike a species, it need not show readily recognizable visible differentiation" (*op. cit.* p. 295). Syngens may differ by a single gene, whereas species do not.

Judged simply as mechanical yardsticks, and irrespective of other qualities, Sonneborn's bases for distinction of his two entities species and syngen are no more and no less satisfactory than the "Mendelian" basis for distinction between species and non-species. Each method sets a reasonably sharp arbitrary limit between two contrasting levels of differentiation, and each lacks complete distinction in the intermediate zone, opening the door to subjective evaluation. "Biological" species differ from the analogous non-species differentiate by having heterosexual reproduction; but there are still extremes between complete heterosexuality and unisexuality or asexuality, as pointed out by Sonneborn (*op. cit.*, pp. 296–297). The borderline between Sonneborn's species and syngen is equally subjective.

My objection to Sonneborn's method as opposed to the "biological" method is simply that at least in organisms that reproduce regularly by heterosexual means the "biological" method comes as close as is possible to the real unit of identification in nature; the Sonneborn species is not an entity, but rather an arbitrary level of differentiation of an entity. The Mendelian species is the entity itself.

Dobzhansky (1950, p. 401) has already lucidly discussed the evolution of Mendelian populations. Species are dynamic —not only the entities but their very organization. It seems reasonable to suppose that the organization of the Mendelian population is the highest form of organization of populational aggregates that has yet evolved. In its present form it is represented by a hierarchy of one, two or three named developmental stages from the heterogeneous population to the cenospecies (Smith, 1955, p. 75). The hierarchy extends from the smallest populational

unit, the *deme* or *panmictic unit*, through a series of any number of larger unnamed populational aggregates to the *hypospecies* (a term introduced to embrace the conventional geographic subspecies as well as macrosympatric but microallopatric *gentes* or strains), then the *plastospecies*, and ultimately the *cenospecies*. Only aggregates at or above the hypospecies level are at the taxonomic level. Mayr's semispecies and superspecies do not belong in this hierarchy since they are phyletic concepts; a semispecies is a member of a family of species (the superspecies) all derived from a common ancestral stock. In the populational hierarchy they might be either plastospecies or cenospecies.

Unisexual organisms have clearly degenerated from the advanced Mendelian organization. Asexual organisms may represent either pre-Mendelian stages of populational evolution or a reversion to Mendelian ancestors; no doubt both exist.

If this view has merit, it must be admitted that the Mendelian species, or unit of identification, cannot possibly be regarded the same as species in organisms with other social organizations. However, as the culmination of evolution, the Mendelian populational hierarchy and the terms and definitions applied thereto may reasonably be utilized as a measure or standard for comparison with other populational hierarchies which should correspond, by analogy, as closely as possible to the Mendelian standard. This premise does, in fact, seem to be a necessary logical sequel to the acceptance of the premises that (1) certain basic units of identification of populations of all organisms be called species, and that (2) the Mendelian hierarchy is the most highly evolved (or "perfect") populational organization. Only if these premises are acceptable is the following discussion valid.

From this point of view, three kinds of populational hierarchies (and therefore three kinds of species since each hierarchy has its species level) embrace all the basic distinctive units of identification needed in the organic world:

1. The Mendelian species and hierarchy,
2. The clonal species and hierarchy,
3. The phyletic species and hierarchy.

The view that wholly different populational hierarchies exist for each of these three structural systems reveals the complete disaster that might result were a different set of names and criteria used for each system. The disaster would lie in the utter confusion of having at least two and in many cases three systems of classification for each organism; there would always be one system based on the phyletic view, and one based on either the Mendelian or the clonal view. Some taxonomic collectives would include both Mendelian and clonal types, and they would thus have to be handled by both of those systems as well as the phyletic system! Sanity demands a single system for identification and classification of organisms.

Clonal and phyletic hierarchies are alike, and differ from the Mendelian hierarchy, in lacking an intrinsic mechanism whereby levels of attainments of differentiation are automatically registered. In the Mendelian developmental system reproductive isolation marks attainment of the species level; in both of the others, differentiation is an absolute continuum without a break in the reproductive continuity. For these species the best possible solution is the criterion suggested by Sonneborn, namely the attainment of the minimal irreversible discontinuity: an expression of the approximate level of differentiation of Mendelian *phaneric* species. As is discussed below it would be unreasonable and impractical to draw the line for species in the phyletic and clonal hierarchies at the level corresponding with the Mendelian sibling species, as Sonneborn has so emphatically demonstrated.

The developmental system of the Mendelian species involves the subspecies in many cases, although that stage is no doubt often omitted in given evolutionary sequences. Yet it does commonly exist as

an intermediate stage between the heterogeneous population and the cenospecies. Since recognition of this stage is irrevocably well established in the systematics of Mendelian populations, recognition of that level as well as the species level itself in the clonal and phyletic evolutionary sequences is in order. Cryptic species of the Mendelian system necessarily must be recognized, but the equivalent thereof (designated syngen by Sonneborn) in asexual and unisexual organisms could most reasonably be designated subspecies in maintenance of Mendelian terminology for analogous stages in clonal and phyletic species. Thus host-specific variants of what is most conveniently called a species could be designated subspecies, and intermediate stages between successive phyletic species could likewise be termed subspecies. Sonneborn's varieties of different asexually reproducing protozoan species would be subspecies.

This approach to species does not eliminate subjectivity, but it does come about as close as possible to objectivity with maximum retention at the same time of the Mendelian reality and terminology. In the most highly evolved population hierarchy (Mendelian), the species is an objective entity with objective parameters; in the intermediate or degenerate hierarchy (clonal), the species is an objective entity but with subjectively determined parameters as closely equivalent as possible to those of the Mendelian populational hierarchy; and in the fourth-dimensional hierarchy (phyletic) the species is a subjective entity with subjectively determined parameters as in the clonal hierarchy.

Thus it must be admitted that the organic species, as a whole (including all three kinds), is subjectively delimited, as indeed critics have maintained, but only because of the universal, acknowledgedly unshakeable, custom-imposed indulgence in the convenience, if not absolute necessity, of a single system for measurement of different things—of a single set of standards for three quite different sorts of units essential to organic identification. The species situation as it thus stands is unfortunate, but it is an inexorable sequel to the evolution of man's knowledge and understanding. Like most complex evolutionary attainments in the organic world, as for example in mammalian structure, the nomenclature of populational aggregates could have been simplified by design, but in fact it was achieved not by starting all over to reach each successive stage of advancement, but by utilizing what was achieved in the preceding stages. Biologists need not be ashamed that their species can be called an arbitrary concept, because it is the pressure of non-biologists as well as biologists that requires retention of a single system of classification for a whole group of basically different things, having in common only that they are made up of organic individuals and need collective names.

Within each of the three wholly different areas of identificational problems, however, the species is a reality, and its parameters in all three areas are established by extrapolation from the complete objectivity that is possible in one area. It is difficult to imagine a more harmonious and realistic resolution of the problem of measurement by one set of standards of variation in three different dimensions. The achievement is comparable to devising a single set of standards to measure weights, areas, and speed. The result is not as satisfactory as starting from scratch and having separate standards for each field of variation, but it is a necessity imposed by irreversible custom, and the end result is surprisingly utilitarian.

REFERENCES

DOBZHANSKY, THEODOSIUS. 1950. Mendelian populations and their evolution. *Amer. Nat.*, *84*:401–418.

MAYR, ERNST. 1957. The species problem. *Amer. Assoc. Adv. Sci.*, Publ. No. 50.

SMITH, HOBART M. 1955. The perspective of species. *Turtox News*, *33*:74–77.

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On Lectotype Proposals

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IN a recent issue of Systematic Zoology (vol. 6: 47-48, 1957) Dr. R. G. Fennah expressed some interesting views on lectotype designations. Fennah's chief objections to the proposed rules for lectotype designation are probably summed up in his statement: "This [referring to an author's freedom to select any one of the syntypes to be the lectotype of a nominal species] means that the great body of classical specimens that have been used as holotypes by generations of taxonomic workers are to be stripped of their authoritativeness unless they are unique or happen to have been mentioned in print as being the only type specimen." This is a harsh indictment and deserves careful consideration.

It seems clear from subsequent discussion in Fennah's article that "the great body of classical specimens that have been used as holotypes" refers to the syntypes labeled "type" in insect collections but not clearly designated in the original publication of the description of the taxon. His criticisms of the proposed lectotype rules are related to the possible effect of the proposed rules on such specimens.

Concerning Fennah's comments on the Distant "type" specimens, of those species for which Distant's publications gave only very limited data, it seems that a taxonomist would logically choose as lectotype the specimen labeled "type," or one of the specimens so labeled, if there were more than one, in the British Museum, the Indian Museum, the Distant collection, the Stockholm Museum, or other repository designated by Distant in the original description in the "Fauna of British India," *provided* that the "type" label was in Distant's handwriting, that it was not on a specimen from a locality not mentioned by Distant in the original description, that the collector's name and the date agreed with those mentioned by Distant (in cases of those species where Distant *did* mention collectors in the original description), and that the designation (in case of mixed series of syntypes) did not violate an interpretation of a first reviser if any of the other syntypes did agree with the first reviser's interpretation. There may be other considerations which would come to mind in making the lectotype selection, but in all likelihood the question of which institution would possess the lectotype would not (and *should not*) be one of them unless all other things were equal. Of the provisions listed above the last (first reviser) is probably the greatest deficiency in the lectotype rules in the unofficial version (Follett, unpublished) cited by Fennah, but he did not mention it. Professor C. J. Bradley's official tentative version of the rules (Bull. Zool. Nomenclature 14, part 16, pp. 142, 143, 1957) has fortunately dealt with this matter and it is to be hoped that his proposal will be adopted.

Fennah goes on to state that Distant [subsequently] discusses his own "types," and raises the question whether these can be interpreted as lectotype designations. They are merely discussions of nonentities, it seems to me, since true types were not formally established originally, nor did Distant manifest any intention of establishing lectotypes. Professor Bradley's well-advised inclusion of the first-reviser principle, however, makes this question academic as far as establishing the identity of the species is concerned, for the subsequent mention of the "types" by Distant (above and beyond whatever diagnostic characters he may have mentioned in connection with them) would narrowly restrict the material from which a conscientious taxonomist would select a lectotype, probably to the specimen or

one of the specimens bearing the "type" label.

Most of the remainder of Fennah's adverse criticisms of the proposed rules on lectotypes are primarily matters of ethics —consideration of the feelings of other workers, choice of lectotypes at whim or at random, and the proper repository of the lectotype chosen—or they have already been taken into account by Professor Bradley's addition of the first-reviser principle (e. g., Fennah's assertion that "the Rules do not require nor even recommend that a reviser consider stability or universality of usage").

There remain Fennah's suggestions for change in the rules. He would have them specify that when "a specimen has been distinctly labeled to distinguish it from all others with the apparent purpose of making it the paramount example of the species, it must be selected as the lectotype, if designation of a lectotype should be necessary." The following possibilities are believed worthy of careful consideration, if such a ruling should be seriously contemplated:

a. Frequently there are several syntypes bearing a mechanically printed "type" label in a given collection. For example, many of E. D. Ball's earlier species are represented in the U. S. National Museum collection by a number of syntypes, each of which bears a "type" label. Any one of these specimens which might have made its way into another collection might be construed to conform to Fennah's suggested rule if a subsequent worker did not know the location of the other syntypes and could not examine them.

b. Where syntype series have been divided among several institutions there have been no restrictions to keep curators other than the author of a species from placing a "type" label on any one of the specimens. Such an action might have violated the intent of the keys and descriptions of the original publication, and in the case of mixed series might even have trespassed the boundary of the tribe in which the species was originally described. Moreover, where a syntype series has been divided between several institutions, the placing of a "type" label on one specimen in each collection might end in the occurrence of *two* (or more) types of a given species, if such a practice is to be tolerated. In this regard, I have been informed by Dr. R. H. Arnett, Jr. (*in litt.*) that there is some duplication of Horn Coleoptera "types" in Philadelphia and the California Academy of Sciences, and some duplication of LeConte Coleoptera types in Philadelphia and the Museum of Comparative Zoology.

c. A curator might label a specimen "type" because it is the only specimen in the collection, because it conforms to the data published with the original description (which may have given a single locality, but no date and no collector), and because the original author's collection is known to be in the curator's care. Perhaps a decade later the remainder of the type series, including a specimen which had been labeled "type" by the original author of the species, may be returned to the institution.

d. A curator might label a specimen "type" in spite of the fact that it bears a locality label not specified in the earlier original description. Is this specimen to be considered authoritative in spite of the published word?

e. A curator might label a specimen "type" in spite of the fact that the species was described by the earlier author only from the other sex. Is such a specimen to be considered authoritative?

f. A first reviser might have accurately diagnosed an earlier author's species in keeping with some of the (mixed) syntype series, but in contradiction to the taxon represented by the specimen labeled "type." If the first reviser's concept has been followed for decades, would Fennah's suggested change in the ruling contribute to stability and universality—or to chaos?

To this writer it seems that the officially proposed version of the rules contributes much more to stability and universality than Fennah's proposed changes. Fennah is undoubtedly correct in wanting selectors of lectotypes to be ethical in their choice of repositories for the lectotypes. Perhaps it would be wise to leave the choice of the repository to the taxonomists who select the lectotypes until the time when they have clearly demonstrated that wrong choices are so common that they need to be legislated against as "illegal" instead of "unethical."

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The Question of Decline in Systematic Activity, Measured in the Marine Amphipoda

J. LAURENS BARNARD

THERE has been an increasing concern in the last two decades that emphasis on systematic biology is on the decline and that in many cases the deemphasis has reached alarming proportions (Chace 1955, Hedgpeth 1955, both articles in: Essays in Honor of Capt. Allan Hancock, Hancock Fd.). Much of this concern has been expressed to the writer verbally and little of it has been documented.

A number of criteria may be used to measure systematic effort, such as the number of published pages, the number of systematic titles (see Reish 1958, Syst. Zool. 7, for a review of the Polychaeta), or in some groups the number of new species described each year. A few groups, *viz.* birds, are so well explored that efforts in the last two decades have been mainly to rearrange known categories into a sensible appreciation of the *New Systematics*. Other groups, such as the mollusks, have a voluminous literature and so many species that an analysis of the systematic effort is a major undertaking.

For these reasons, the gammaridean Amphipoda represent a reasonable group wherein systematic effort over the past two centuries can be approximated. The Amphipoda are a small order of about 4300 species of which the suborder Gammaridea comprises 3200 species. Of these, 2400 are marine and the accompanying analyses concern only the marine species.

It is believed by the writer that descriptive effort in the suborder has not reached a level of diminishing returns, in witness of the recent efforts by Russians in the northwestern Pacific, and workers in the eastern Pacific, New Zealand and west Africa, where the unknown faunas have revealed hundreds of new species in the last decade. The very poorly known continent of South America, the entire Pacific Ocean, Indian Ocean, etc., still provide fertile fields for the discovery of new species.

No bibliography of the Amphipoda has appeared since 1888 (Stebbing, Challenger Repts. 29) but one is in preparation by Dr. D. E. Hurley of New Zealand. The last major treatise on the Gammaridea (without bibliography) was by Stebbing (1906, *Das Tierreich* 21). The writer's recent "Index to the Families, Genera and Species . . ." (Barnard 1958, Hancock Fd. Occ. Pap. 19) of the Gammaridea lists about 3200 species, an increase of about 2000 valid species since 1906.

Figure 1 was compiled from the 1958 Index which is complete to 1956. It shows the valid species of marine Gammaridea described in each half decade since 1829, the species later relegated as synonyms, and cumulative totals of valid and total species described. These figures are self-explanatory. The cumulative totals include all species since 1758.

Figure 2 is an approximation of work effort in the group and number of existing specialists in any half decade since 1829, based on my bibliographic files. Work effort has been based on the number of pages published by major workers. A major worker is one who published 5 papers or 50 pages in any half decade. All

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FIG. 1

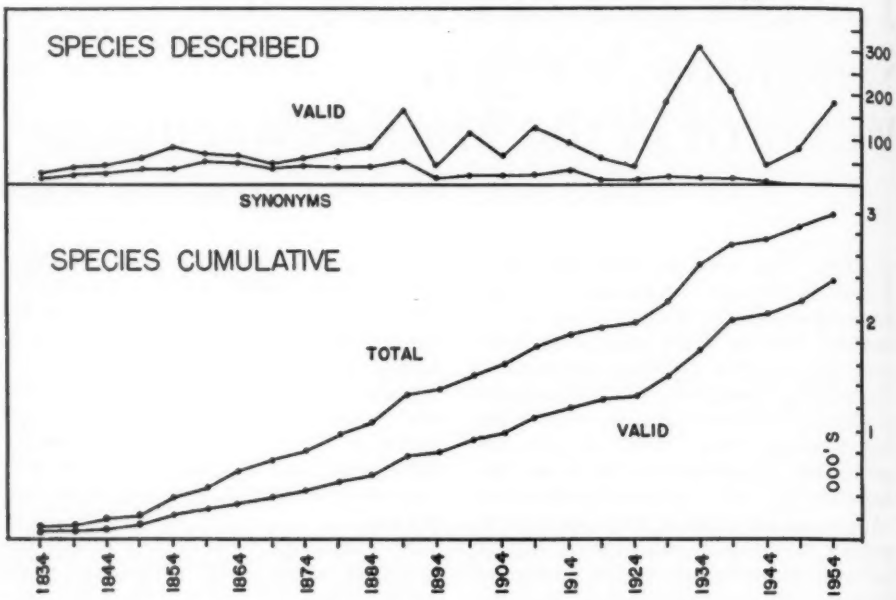
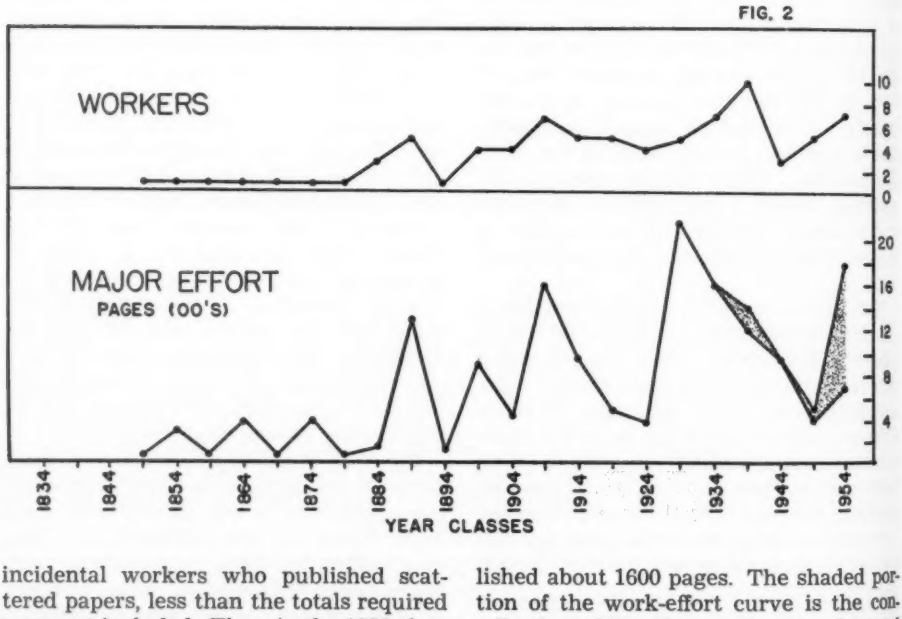


FIG. 2



incidental workers who published scattered papers, less than the totals required were not included. Thus, in the 1939 class there were 10 major workers who published about 1600 pages. The shaded portion of the work-effort curve is the contribution of Russian workers to the total world effort, which amounted to 60 per

cent in the 1954 class. According to this analysis no half decade prior to the 1934 class produced a major Russian worker or work effort in marine amphipods, although these occurred in freshwater work several times (Lake Baikal).

It might be assumed that a major worker in the field of amphipod systematics was devoting his full time to the group but that is scarcely the case. For instance, I was included in the 1954 class as a major worker, but devoted only about one-half of my time to the group. I will be considered a major worker in the 1959 class but have devoted less than one-fifth of my time to amphipods. This condition appears to be the case with most of the other major workers, determined from my correspondence with them and from an appreciation of their published efforts in other fields.

During the decades of 1920 and 1930 there were several workers, estimated by me to be four, devoting nearly all their time to amphipod systematics. In this decade (1950) I know of only one. In the United States there are two active systematists but their combined output in amphipods is about one-sixth the output of the four or five Russian systematists.

The amphipod fauna of the northeastern Atlantic is very well known, so that diminishing returns govern the low systematic output there. As a result, the concentration of work centered there between 1870 and 1910 has moved afield; European workers in the 1920–1940 period concentrated on antarctic and tropical faunas. Most of these workers are no longer active. The concentration of effort has moved to the northwestern Pacific (Russian) where activity has been intense and diminishing returns may be expected in the next decade. New Zealand and California have been activated in the last decade but the rate of work indicates no diminishing returns for the next two or three decades. The entire tropical belt and South America offer fruitful exploration and the Antarctic remains to be reconsidered. Progress in abyssal faunas is satisfactory.

Despite the facts that the rate of new descriptions is recovering from the War II slump (Figure 1) and the work effort has recovered to more than 80 per cent of the 1929 peak (Figure 2), activity in the Amphipoda, as measured by new descriptions, has a prognosis of decline in the next three decades. Sixty per cent of the effort is Russian and this intensity should meet diminishing returns if the Russians confine their activities to their own seas. The general apathy toward this work in America measured by the attitudes of most marine laboratories (Hedgpeth, 1955) and the low paying or non-existent positions in museums, plus the lack of trained personnel, offers little favorable prognosis for American leadership. The United States has had only one outstanding worker in the field (C. R. Shoemaker), his work covering the last four decades. In terms of population New Zealand now produces at a rate of 30 times that of the United States and can scarcely justify more workers on that basis. Australia, South America and the Asian countries could justify a large increase in their efforts, both by population and by unknown faunas. The western European nations have overextended their generosity to this field in the last century.

With the exception of the three or four above-mentioned active areas, contributions to amphipod systematics have declined from the two great periods (1870–1910 and 1925–1935) where faunas of large areas were compiled to a level where the remaining faunas are being considered casually and haphazardly (witness the large number of one genus-one species papers).

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Points of View

CHARACTER SELECTION IN SYSTEMATICS WITH SPECIAL REFERENCE TO THE CLASSIFICATION OF LEAFHOPPERS (INSECTA, HOMOPTERA, CICADELLOIDEA)

In a recent issue of this journal there appeared an article by H. H. Ross entitled "Evolutionary Developments in Leafhoppers," in which a new classification was proposed for this group of insects. The new system is based very largely on characters which have not previously been used as indicators of possible inter-relationships (Ross, 1957).

Almost all the suggestions which Ross has made differ from those formerly proposed by myself and since in his paper he makes frequent reference to my work, it would seem that some comment from me is necessary, as otherwise silence might be misconstrued as concurrence.

If a system of classification of the higher categories of a group of organisms of wide distribution is intended to express natural relationships and not merely be one of convenience, as well as long apprenticeship, it calls for a knowledge of representatives of the group on a world-wide basis. Otherwise it is probable that too much weight may be given to characters of limited significance and not enough to others of great importance.

It is my opinion that wing venation, when correctly analysed and interpreted, is the most important fundamental character for indicating leafhopper relationships at family level, and the next most significant one is provided by a balanced analysis of head structure and shape. However, as with any other characters, these need to be used only as guides to relationships, which before receiving acceptance require support from evidence furnished by other morphological features.

Ross has paid no attention to wing venation and the information he has given about cephalic sutures, whilst doubtless correct for the Nearctic fauna, is not generally applicable on a wider basis.

The characters he has chosen as phylogenetic critera are noted and commented upon below.

Mesosternum. He has shown that in the Cicadellidae the mesosternum is separated from the pleurae by a sternopleural suture in all but one aberrant subfamily, but in the Membracidae this suture is obliterated. He has also pointed out that except in the Ulopinae and Cicadellinae the mesosternal suture is Y-shaped, and if I have interpreted his remarks correctly, he implies that the condition of the sternum in the Ulopinae is a secondary development.

Kramer (1950) has previously shown that the suture which in cicadellids separates the anepisternum from the pre-episternum is lacking in membracids and this certainly is an important differentiating character. In regard to the sternum itself, I suggest that the development shown by Ross in his Figure 2, C, for the Ulopinae, represents an earlier condition than that illustrated in his Figure 2, E, in which a Y-suture is present.

Mesonotum. Ross suggests that there is a fundamental difference between cicadellids and membracids because of the development in representatives of the latter family of a new transverse scutal suture, accompanied by the loss of a more anteriorly placed one.

To the extent that an anteriorly placed U-shaped area and its accompanying transverse sutures (which indicate zones

of separate muscle attachments) have become obliterated in the Membracidae, his observations, which so far as I am aware have not previously been recorded, are correct. However, in the Aetalionidae these sutures are not entirely lost and in many cicadellids the posterior ones are present and well defined, even though those from the two sides do not so closely meet medially as happens in membracids. In some cicadellids (e.g., *Coloborrhis* spp.) there is a complete transverse suture which separates the scutellum from the rest of the mesonotum, but this fact does not necessarily imply that it is of particular value as a phylogenetic character.

Head. Ross states that in most cicadellids the junction of the arms of the epicranial suture with the stem of the same suture is obliterated. Also, that the epistomal suture is present in Membracidae and Cercopidae but that in the Cicadellidae it is either lost or else its identity is extremely doubtful.

As may be seen from illustrations I have given of the heads of cicadellids (Evans, 1947), complete Y-shaped epicranial sutures occur in representatives of no less than eight subfamilies.

In regard to the epistomal suture, while, as Ross has stated, it is present in the Cercopidae, it is by no means always discernible in the Membracidae but it may be clearly distinguished in representatives of twenty tribes or subfamilies of the Cicadellidae.

Hind leg. Ross has noted that in three groups of leafhoppers, the Eurymelidae, Hylicidae, and Ledrinae (Cicadellidae), the hind tibiae have "a lateral row of large spines each with a macroseta or hair set in it" while in other groups of leafhoppers (apart from the Membracidae, in which he includes the Aetalionidae) "the tibia has a lateral row of large macrosetae each set in a large basal socket."

It is true that some hylicids, though not all, have spines mounted on prominent spurs and that all eurymelids, apart from the myrmecophilous Pogonoscopinae, have one or more large spurs on their robust hind tibiae, and that likewise spurs are to be found on the usually flattened hind tibiae of ledrids. It is also correct to state that such spurs do not occur on the hind tibiae of other leafhoppers. At the same time, this fact, when unsupported by evidence of any other sort, would seem to provide an inadequate reason for proposing a natural grouping in a high level category.

In regard to the spines situated close to the apex of the hind femora, as Ross has stated, these have previously been used by Ribaut (1952) for the separation of some groups of European leafhoppers and it is evident that they are of some taxonomic importance, so long as their significance is viewed in proper perspective. These spines are not of universal occurrence even within the Cicadellidae since they are lacking from the hind femora of certain ulopids.

Phylogenetic Tree

In the phylogenetic tree that Ross suggested for the Cicadellidae there are four principal branches. The first comprises his division Eurymelides in which are grouped together the Hylicinae, Eurymelinae, and Ledrinae. The two former I have regarded as distinct families and the third as a subfamily of the Cicadellidae. His next series, the Xerophloeides, contains a single genus, *Xerophloea* Germar, while the two others, the Macropsides and Tartessides, comprise four and fourteen cicadellid subfamilies respectively. These last named are largely, though not exclusively, ones which have representation in the Nearctic region. Before considering each of these divisions in turn it is necessary to pay some attention to the superfamily Cicadelloidea as a whole and its position within the Homoptera.

The Homoptera are usually separated into three principal series, one of which is known as the Auchenorrhyncha. This series comprises four natural superfamilies, the Fulgoroidea, Cicadoidea, Cerco-

poidea, and Cicadelloidea. These may be segregated into two natural divisions, one the Fulgoromorpha containing the Fulgoroidea, and the other, the Cicadomorpha, containing the remaining superfamilies (Evans, 1951).

Cicadas differ from both cercopoids and cicadelloids in having a median ocellus, and nymphs that lead a subterranean existence and have their forelegs modified for digging purposes.

Cercopoids (spittle bugs) differ from cicadelloids (leafhoppers) in numerous features of which two are the nature of the tentorium, and the structure and way of life of the nymphs. It would seem, if the fossil record has been correctly interpreted, that these two groups have been distinct since at least Upper Permian times (Evans, 1956, 58).

Not only do membracids and cicadellids share the cephalic character mentioned above, which is a discontinuity between the anterior and posterior arms of the tentorium, but they also have the same basic arrangement of the veins of their forewings (Evans, 1948). In both of these characteristics, in which they resemble each other, they differ from the Cercopoidea.

Ross has stated that I have segregated a number of aberrant genera of leafhoppers into three families, namely the Aetalionidae, Hylicidae, and Eurymelidae, and further that these families are intermediate between the Cicadellidae and Membracidae. These families were defined in 1946 (Evans, 1946, *a, b*) but I have never regarded them as linking the Cicadellidae and Membracidae. Recently (Evans, 1956) I have indicated in a chart my present views on their relationships with each other and also with two other families of leafhoppers, the Nicomiidae and Biturritidae (formerly Lampropteridae) (Evans, 1948).

At one time leafhoppers were separated into groups largely on the basis of the position of their ocelli. Thus, those with ventral ocelli were placed in one subfamily, those with marginal ocelli in another, and those with dorsal ocelli in yet another. For leafhoppers that seemed to be outstandingly aberrant and not to fit into any of the above categories, separate subfamilies or even families were created.

This system, which was based primarily on the Palaearctic fauna, broke down and became meaningless when applied to the leafhopper fauna of the world as a whole. The reason was not that the position of the ocelli is never of any significance as a taxonomic character, but only that, like any other morphological feature, its importance can be assessed only when it is considered together with other characters. Thus, while a system of classification that is based on the consideration of a single character, or even of several characteristics of which the significance is not understood, may express true relationships, it is more likely to do otherwise, especially when higher categories are concerned.

Although Borgmeier (1957) is of the opinion that systematics should be unconcerned with time and space, fossil evidence and facts of geographical distribution do frequently provide helpful subsidiary evidence for use in establishing systems of classification, and certainly this is the position so far as leafhoppers are concerned.

The earliest known leafhoppers (Archescytinidae), which have been recorded from Lower and Upper Permian strata, had forewings in which, in their basic condition, seven veins served to support the apex of the wing.

These veins were as follows: *R1b, Rs, M1, M2, M3, M4* and *Cu1a*. From this family I have suggested that two others (the Syctinopteridae and Prosbolidae) were derived (Evans, 1956). Both of these are represented in rocks of Upper Permian and Triassic age and their forewings resemble each other and also those of the Archescytinidae, in having seven veins extending to the apex of the wing.

The Prosbolidae differ from the Scytinopteridae in having a transverse line of

weakness which enables the apex of the forewing to be flexed downwards. This feature, the nodal line, is retained by most cicadas at the present day.

Apart from the Aetalionidae which have reticulate venation, and the Nicomiidae which is a small relict group, all recent cicadelloids have a basic venational pattern in which only four veins support the apex of the forewing, but these veins are not of identical derivation in the various groups. In the Cicadellidae and Membracidae they consist of *R1b, Rs+M1+2, M3+4* and *Cu1a;* in the Eurymelidae of *R1b, M1+2, M3+4 and Cu1a,* and in the Hylicidae *of R1b, Rs, M1+2, M3+4+Cu1a.*

The suggestion provided by wing venation that the Cicadelloidea comprise six natural major groupings is supported not only by numerous other structural factors, but also by ones of space (geographical distribution). Particulars of these latter have been given elsewhere; for the present purpose it is sufficient to mention a few only of the former in order to emphasize the distinctiveness of the Hylicidae and the Eurymelidae and also the fact that the Membracidae are not such an isolated group as is so often supposed.

The Eurymelidae, like the Membracidae, are gregarious insects and in their male genitalia the aedeagus lacks direct association with the basal connective that lies between the paired parameres or harpogones, but in all other leafhoppers the aedeagus is in contact with the basal connective.

The forewings of many hylicids retain evidence of the presence of a nodal line, which suggests that they have been derived from a prosbolid stock, unlike other leafhoppers, which I have assumed are of scytinopterid descent. Then, as well as having scales and hairs on their bodies, a development lacking in other leafhoppers, they have an unusually extensive development of the thorax.

As the cicadellid subfamily, the Ledrinae, is included by Ross in his division Eurymelides, it too requires brief notice. The Ledrinae resemble the rest of the Cicadellidae and differ from the Eurymelidae and Hylicidae in the characters of venation, male genitalia, and thoracic development which have already been mentioned, and differ from the Eurymelidae also in the position of their ocelli, and from the Hylicidae in other cephalic features. Thus, in the Ledrinae the ocelli are always situated on the crown of the head, whilst in the Eurymelidae they are always facial in position. The Ledrinae never retain prominent antennal ledges and usually have the anterior tentorial pits exposed. Both the Eurymelidae and Hylicidae have distinct antennal ledges, but never a readily discernible anterior tentorial pit.

It is hoped that the foregoing remarks will serve to show that the division Eurymelides, which Ross has established to group together those leafhoppers which have some of the spines on their hind tibiae mounted on enlarged spurs is more an arrangement of convenience than one expressing close natural relationships.

Xerophloeides. Although I placed *Xerophloea,* which is represented solely in the Western Hemisphere, in the subfamily Ledrinae (Evans, 1947), I have been aware that it has certain anomalous features that separate it from other genera in this subfamily. It is for this reason that I have suggested that, together with other distinctive genera, it might merit subfamily differentiation (Evans, 1951). On the other hand it is quite certain that its special characteristics are not of such an outstanding nature as to call for its elevation to the status of a separate division commensurate with the others that have been proposed by Ross.

Macropsides. In this division Ross has placed the Idiocerinae, Macropsinae, Agalliinae, and Ulopinae and to the extent that these four subfamilies all lie close to the base of the cicadellid stem, it is a natural grouping. A character which Ross attributes to the Idiocerinae, that ledges above the antennae are lacking, is not of

universal occurrence within this subfamily. Likewise, his observation that the Macropsinae lack epicranial sutures above the antennae cannot be applied to all representatives of this group. If a morphological comparison is made between the macropsids, *Stenoscopus* Evans and *Stenopsoides* Evans (both illustrated in Evans, 1947), the biturritids, *Endoiastus* Osborn and *Melizoderes* Blanchard (illustrated in Evans, 1948) and representatives of the Ulopinae (Cicadellidae) and Centrotinae (Membracidae) it will be appreciated that there are certain overlapping characteristics in these various groups which suggest that they have a close degree of relationship. Thus, on the basis of pronotal development *Stenopsoides* could be considered a membracid, and on the basis of head structure *Endoiastus* might be placed in the Ulopinae. Yet a balanced view of their several attributes suggests that such action would confuse, rather than clarify, leafhopper classification. In other words it is possible to erect any number of possible combinations of genera on the basis of some common characteristics but to do so may not have the effect of advancing knowledge.

Ross follows Oman (1949) in regarding the Megophthalmini as a tribe of the Agalliinae. This presumably is due to preoccupation solely with the Nearctic fauna. Reference to illustrations of species in the genus *Evansiola* China, which both China (1955) and myself (Evans, 1957) regarded as belonging to the Megophthalmini will indicate that the relationships of this tribe are closer to the Ulopini than to the Agalliinae.

Tartessides. This assemblage includes the remaining subfamilies of leafhoppers which have representatives in North America, together with a few additional ones from elsewhere. Ross has re-united the Neocoelidiinae with the Coelidiinae into a single subfamily and while very possibly this combination may be justified on the grounds of genetic affinity, I would regard it as a retrograde step since it serves to obscure the very distinctive features of the former group.

In regard to the remaining associations of subfamilies that are indicated by Ross in his tree, comment is for the moment withheld until such time as I, and I hope also others, have had the opportunity of assessing their true significance. Meanwhile it is suggested that it is improbable that *Nionia* Ball has close affinity with the Nirvaninae, or that this latter subfamily is derived from the same stem as the Jassinae.

In conclusion it needs to be acknowledged that while I cannot accept most of the proposals made by Ross on leafhopper classification, this does not infer that I am so satisfied with my own suggestions on the same topic that I consider that they are in no need of revision. However, advances that can lead to a better understanding of this ancient, complex, and most interesting group of insects can only be expected as a result of studies based on the prerequisities mentioned at the beginning of this article and not from an approach which depends on unweighted character selection.

REFERENCES

BORGMEIER, T. 1957. Basic questions of systematics, *Syst. Zool.*, *6*:53–69.

CHINA, W. E. 1955. A new genus and species of Ulopinae from Juan Fernandez Islands. *Rev. Chil. Ent.*, *1955* (4):199–203.

EVANS, J. W. 1946,*a*. A natural classification of leafhoppers. *Trans. R. ent. Soc. Lond.*, *96*:47–60.

——— 1946,*b*. A natural classification of leafhoppers, Pt. 2. *Trans. R. ent. Soc. Lond.*, *97*:39–54.

——— 1947. A natural classification of Leafhoppers, Pt. 3. *Trans. R. ent. Soc. Lond.*, *98*:105–271.

——— 1948. Some observations on the classification of the Membracidae and on the ancestry, phylogeny and distribution of the Jassoidea. *Trans. R. ent. Soc. Lond.*, *99*: 497–515.

——— 1951. Some notes on the classification of leafhoppers with special reference to the Nearctic fauna. *Comment. Biol.*, *12*(3):1-11.

——— 1956. Palaeozoic and Mesozoic Hemiptera. *Aust. J. Zool., 4*:165–258.
——— 1957. Los insectos de las Islas Juan Fernandez. 28. Cicadellidae. *Rev. Chil. Ent., 1957* (5):365–374.
——— 1958. New Upper Permian Homoptera from the Belmont Beds. *Rec. Aust. Mus., 14*:109–114.
KRAMER, S. 1950. The morphology and phylogeny of the auchenorhynchous Homoptera. University of Illinois Press. 78 pp.
OMAN, P. W. 1949. The Nearctic leafhoppers. *Mem. Ent. Soc. Wash., 3*:1–253.
RIBAULT, H. 1952. Homopteres auchenorhynques. II (Jassidae). *Faune de France, 57*:1–474.
Ross, H. H. 1957. Evolutionary developments in leafhoppers. *Syst. Zool., 6*:87–97.

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THE TERMS TERGUM AND STERNUM, TERGITE AND STERNITE

If one were to look through the current numbers of our entomological journals, with the above terms in mind, he would scarcely fail to note that almost invariably systematists use tergite and sternite when referring, respectively, to the *whole* dorsal or *whole* ventral plate of a single abdominal segment. He would note, too, especially when a thoracic segment is being dealt with, that these same terms are used frequently to denote one of the *component sclerites* in these two areas of a segment; and yet, of course, a thoracic segment is strictly homologous with an abdominal one. Obviously, the use of any term in two wholly different senses is open to serious objection—especially if we already have accepted terms for use in each sense. To state the matter in another way, if a "tergite" can be composed of tergites and a "sternite" of sternites, something is clearly wrong with either our terminology or our usage.

There appears to be no disagreement among our leading morphologists with reference to what the terms mean. I have taken Imms, Snodgrass, and Comstock as my entomological authorities, partly because their works happen to be immediately available, but principally because there can be no dispute regarding their eminence as morphologists; and for comparable reasons I am using a leading biology text and a prominent zoology one, for the purpose of presenting the case below.

All three of the entomological authorities are perfectly consistent in their definition and usage of the four terms, tergum, sternum, tergite, and sternite. Imms, on page 11 of the 1925 edition of his text, says. "The body of an insect . . . is divided into a series of successive rings. . . . With the exception of many insect larvae, which have a non-chitinized cuticle, the wall of each segment is divisible into four definite chitinized regions: a dorsal region or tergum, a ventral region or sternum, and a lateral region or pleuron on each side of the body. Each of these regions may be differentiated into separate sclerites. In this case the sclerites composing the tergum are known as tergites, those of the sternum as sternites and those constituting each pleuron as pleurites." He uses these terms, as defined, throughout his book; and in his figures, such as that of a staphylinid beetle on page 461, labels the individual dorsal segmental plates of the abdomen as terga—not tergites.

Snodgrass, on page 82 of his book on insect morphology, defines these terms as follows:

Tergum.—The dorsal sclerotization of a body segment; called also notum, especially in the thorax.

Tergite.—A subdivision of a definitive tergum, or any one of several sclerites in the dorsum of a body segment.

Sternum.—Either the primary ventral

plate of a body segment or a composite definitive sternum.

Sternite.—A subdivision of a sternal plate, or any one of the sclerotic components of a definitive sternum.

On page 71 he defines these terms in less technical language by saying, "A major segmental plate of the dorsum is a tergum, or notum; a major segmental plate of the venter is a sternum; plates of the pleural areas are designated pleural sclerites. Subdivisions of a principal segmental plate or the component sclerites of a major area of sclerotization, then, become tergites, sternites, and pleurites, respectively, since the suffix -ite has a fractional significance." Scores of illustrations on following pages attest his consistent use of this terminology, and Figure 139 on page 251 makes clear the differences between these terms when they are applied to the parts of an abdominal segment.

Comstock's definitions of the same terms differ in no essentials from those of Imms and Snodgrass. In his brief discussion of the fundamental plan of each of the twenty or so homologous segments which make up the body of an insect, he says on page 34, "The larger divisions of a segment that are commonly recognized are a dorsal division, the tergum; two lateral divisions, one on each side of the body, the pleura; and a ventral division, the sternum. Each of these divisions may include several definitive areas of chitinization. In this case the sclerites of the tergum are referred to collectively as the tergites, those of each pleurum, as the pleurites, and those constituting the sternum, as the sternites." These statements are re-inforced on page 75, where he treats of the segments of the abdomen. Here he says, "The body wall of an abdominal segment is usually comparatively simple, consisting in adults of a tergum and a sternum, united by lateral conjunctivae."

Even in the elementary biology texts, such as Mavor's, written primarily for freshmen biology students, we find the same definitions. On page 375, in treating of the grasshopper, Mavor says, "The exoskeleton of a typical metamere, seen best in the abdomen, consists of a dorsal portion or tergum and a ventral portion or sternum."

Storer's textbook on general zoology, also written for beginning students, in discussing the general features of the crayfish on page 467, says, "The skeletal elements of a single somite, as in the abdomen, include a transverse dorsal plate or tergum, and a ventral crossbar, or sternum"; and later, on page 489, he says of the abdomen of the grasshopper, ". . . somite 8 resembles those preceding, the terga of 9–10 are fused, and the tergum of 11 forms the suranal plate. . . . In a female . . . the sternum of 8 is apparently lacking. . . ."

From what has been said above, it is apparent that our morphologists, biologists, and zoologists appear to be in agreement on the application of these terms, and there would seem to be no cogent reason why entomological systematists should not similarly apply them. Certainly our students at the college level are properly taught in courses which deal with the anatomy of the insect. Are they later mislead by custom if they become taxonomists?

Perhaps one cause of these inconsistencies may be that many entomologists accept as correct *all* of the definitions given by J. R. de la Torre-Bueno in his much-used glossary. The purpose of this work, as he clearly stated in his introduction, was solely to reflect usage and not to set standards. He thus made no attempt to distinguish between good or preferred usage and poor or incorrect usage; yet many entomologists refer to it for authoritative information on entomological terms. This habit must certainly have perpetuated much poor usage and has doubtless tended to fix some of it.

So much time is wasted in trying to find out the meanings of new terms which are not in our latest unabridged dictionaries or even in our special glossaries, that we

should not be handicapped additionally by a tendency to make certain terms ambiguous. Clearly, the cure is not the substitution of a third term in an attempt to remove the ambiguity, as has been done in certain instances, but the proper employment of the terms that we already have.

REFERENCES

COMSTOCK, JOHN HENRY. 1930. An introduction to entomology (revised edition). Comstock Publishing Co., Ithaca, N. Y.

IMMS, A. D. 1925. A general textbook of entomology. Methuen, London.

MAVOR, JAMES WATT. 1953. General biology (fourth edition). Macmillan, New York.

SNODGRASS, R. E. 1935. Principles of insect morphology. McGraw Hill, New York and London.

STORER, TRACY I. 1951. General zoology (second edition). McGraw Hill, New York, Toronto, and London.

TORRE-BUENO, J. R. DE LA. 1937. A glossary of entomology. Science Press, Lancaster, Pa.

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IN REGARD TO NEMA THE THREAD

Chitwood's attempt (Systematic Zoology, December, 1957) to force the term nema in place of nematode on zoologists is specious and unconvincing. It is impossible to make sense of the claim that nematode is an unsuitable word because it is derived from Nematoidea. So is cestode derived from Cestoidea but nobody has thereby suggested that cestodes should be called cests. Some other possibilities along this line are anns for annelids and molls for mollusks. The replacement of nematode by nema is offensive because the word nema lacks scientific dignity; it smacks of being a nickname "for short," and in fact there is no doubt that Cobb promulgated nema in an attempt to popularize the study of these worms.

One is flabbergasted at the assertion of Cobb that nema has been a household word for thousands of years. One asks, in what households? Is nema an English word? It seems to be pure Greek. Furthermore nema was already long in use for a structure in graptolites that is honestly threadlike. Although there is little possibility of confusion here, zoology should be purged of such homonyms.

Chitwood has not shown leadership in correcting various abuses of terminology in nematodes. In his *Introduction to nematology* he continued to call the epidermis hypodermis, the pharynx esophagus, and juvenile stages larvae, although he admitted that the last usage is erroneous. His attempt to call the buccal capsule stoma was preposterous. Stoma is no doubt another good old English household word but it means mouth and cannot be made to mean something else.

Chitwood's real purpose is obviously to replace Nematoda by Nemata as a class (or phylum?) name. I regard the creation of new names for the identical groups for which good names long in use already exist as unethical. Cobb's name Nemates was unjustifiable and headed a scheme of classification so obviously foolish that nobody has paid any attention to it.

I grant that nema combines better than nematode in one or two cases. It is probably impossible now to displace the incorrectly formed terms nematology and nematologist. But the other suggestions of Chitwood, as nematize, denematize, nematization, and nematosis, are abominable.

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UNIFORM ENDINGS FOR THE NAMES OF HIGHER TAXA

The botanists long ago adopted a system of uniform endings for the names of their higher taxa, but zoologists have never been able to agree on one. In a report prepared for Section F of the American Association for the Advancement of Science, Pearse (1936) suggested the following endings: Phylum and Subphylum, -a; Class, -ea; Subclass, -ia; Order, -ida; Suborder, -ina. In doing so he remarked that he might be a hundred years ahead of his time. Almost a quarter of this span has passed, and there is no evidence that Pearse was wrong in his estimate.

Stenzel (1950) proposed the following endings: Superorder, -ica; Order, -ida; Suborder, -ina; Superfamily, -icae; Family, -idae; Subfamily, -inae; Supertribe, -ici; Tribe, -idi; Subtribe, -ini. This provoked a flurry of criticism (Simpson, 1952; Hubbs, 1952) and some support (Rogers, 1952; Moment, 1953), but there has been little progress since. Mayr, Linsley and Usinger (1953) felt that ordinal names such as Primates, Carnivora, etc. were much too well established to be upset for the sake of uniformity. At the Colloquium on Zoological Nomenclature held in Copenhagen in 1953 (Hemming, 1953), it was decided that (Par. 67) "The Colloquium is of the opinion that there should be no prescribed terminations for the names of taxa belonging to the Order/Class-Group and the Phylum-Group." The discussions which led to this statement were not reported. No regulations for the nomenclature of higher taxa were included in the New Code adopted by the Colloquium on Zoological Nomenclature held in London in 1958 (*in press*).

There is no question concerning the advantages of a system of uniform endings. It would be simple, logical and consistent. Even the beginning student would know the rank of each taxon at a glance, an impossibility under the present chaotic system. Moment (1953), for example, gave the following incomplete list of endings now used for the names of orders: -ura, -ptera, -ida, -ozoa, -aria, -icha, -ina, -ora, -acea, -oela, -dela, -chia, -ata, -iformes, -tia, and -pha.

I pass over as hardly worth refuting the objection that the new system would be somewhat bothersome to the present generation of taxonomists. The same objection was raised, I am sure, to the change-over from Roman to Arabic numerals.

Another objection, the fear that many time-honored names like Rodentia, Edentata, Primates and Carnivora would disappear, is groundless. Their endings would be changed, but the old familiar stems would be retained—a rat would still be a rodent.

The most serious objection is not against the idea of uniform endings *per se*, but against the particular ones proposed. It is that they would be a new source of confusion. For instance, as Hubbs (1952) pointed out, if there were an order Poeciliida and a family Poeciliidae, we would not know which was meant when someone wrote familiarly about poeciliid fish.

It would be a simple matter to avoid this pitfall by selecting readily distinguishable endings. The following endings would be such: Superclass, -asica; Class, -asida; Subclass, -asina; Superorder, -orica; Order, -orida; Suborder, -orina; Superfamily, -icae; Family, -idae; Subfamily, -inae; Supertribe, -ibica; Tribe, -ibida; Subtribe, -ibina.

This set of endings would differentiate not only major levels in the taxonomic hierarchy, but also, by making use of parallel structure, minor ones (i.e., super- and sub-categories). Major levels are indicated by two-letter vowel-consonant combinations immediately following the stem (except in the case of Family-Group endings). The Class-Group is designated by -as-, the Order-Group by -or-, and the Tribe-Group by -ib-. Minor levels within each group are then designated by the last two syllables.

Other major level indicators such as -icoh-, for Cohort-Group could be used if desired.

Some examples will illustrate the application of these endings. In the case cited by Hubbs (1952), the order would be Poeciliorida, the family Poeciliidae, and the corresponding familiar terms would be poeciliorid and poeciliid. A number of already existing ambiguities of this type would also be cleared up. For example, among the Nematoda there is now a suborder Strongylina and a subfamily Strongylinae, both of whose members have been referred to as strongylines. Under the proposed system the suborder name would be changed to Strongylorina and its members could be referred to familiarly as strongylorines.

Under the proposed system the protozoan order Entodiniomorpha would become Entodiniorida, the avian order Anseriformes would become Anserorida, the mammalian order Rodentia would become Rodentorida, the mammalian order Primates would become Primatorida, the insect order Diptera would become Dipterorida, the insect order Orthoptera would become Orthopterorida, and the cestode order Tetrarhynchoidea would become Tetrarhynchorida. The protozoan class Zoomastigophorea would become Zoomastigasida, the class Insecta would become Insectasida, and the class Mammalia would become Mammaliasida. The nematode superfamily Strongyloidea would be Strongylica, a change which would end the confusion between the name of this superfamily and that of the genus *Strongyloides*, which belongs not only to a different superfamily but to a different suborder.

The present confusion could be ended if the above uniform endings or a similar series were generally adopted. It is hardly to be expected that this system would be adopted immediately by everyone, but if enough people considered it worthwhile and began to use it, its eventual acceptance would be easy. It is therefore presented for use by those who wish to use it. Some of the new names might look a little queer at first, but taxonomists should have no more difficulty than brides in getting used to them.

LITERATURE CITED

HEMMING, F. 1953. Copenhagen decisions on zoological nomenclature. International Trust for Zool. Nomenclature, London. pp. xxix + 135.

HUBBS, C. L. 1952. On uniform group endings. *System. Zool., 1*:146–147.

MAYR, E., LINSLEY, E. G., and USINGER, R. L. 1953. Methods and principles of systematic zoology. McGraw-Hill, New York. pp. ix + 328.

MOMENT, G. B. 1953. Uniform endings and the revival of interest in taxonomy. *System. Zool., 2*:191–192.

PEARSE, A. S. 1936. Zoological names. A list of phyla, classes, and orders. Duke Univ., Durham, N. C. pp. 24.

ROGERS, D. J. 1952. On uniform endings. *System. Zool., 1*:147–148.

SIMPSON, G. G. 1952. For and against uniform endings in zoological nomenclature. *System. Zool., 1*:20–23.

STENZEL, H. B. 1950. Proposed uniform endings for names of higher categories in zoological systematics. *Science, 112*:94.

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Books in Brief

INDEX TO THE FAMILIES, GENERA, AND SPECIES OF THE GAMMARIDEAN AMPHIPODA (CRUSTACEA). By J. Laurens Barnard. Allen Hancock Foundation, Occ. Paper No. 19, University of Southern California Press, Los Angeles, California, 1958. 145 pp. $1.25 (Paper Bound).

SINCE the publication of T. R. R. Stebbing's monograph (Das Tierreich, Vol. 21, 1906) the number of accepted species of gammaridean Amphipoda has increased from 1241 (in 317 genera and 41 families) to 3150 (in 600 genera and 57 families). The sizable task of providing an up-to-date reference source of valid names and nomenclatural additions and changes in this large crustacean group has been successfully accomplished in J. L. Barnard's *Index*. The specialist and non-specialist alike will readily appreciate the concise form of this easily accessible and compact booklet. It contains an alphabetical list of families and genera, and a generic index that indicates (by number) not only the family to which the genus is currently assigned, but also the family from which it may have been transferred, and whether or not it has been fused with another genus. In addition, the catalogue provides a detailed index, also alphabetical, to the species (by family and genus), that lists accepted names, synonymies, and names transferred to other genera. The selected bibliography of about 40 important publications since 1906, along with the *Zoological Record* (1900–1954), is intended to provide at least one published reference to every specific, generic, or family name contained in the catalogue. The name of each species described since 1906 is accompanied by the name of the author and date of publication, that published prior to Stebbing's monograph by only the author's name and letter "S."

The author is to be commended for his skill in compressing a large amount of reference material into such an abbreviated but useful form. His decision not to treat subgeneric or subspecific names unless subsequently elevated to full generic or specific status, coupled with his limited selection of post-*Zoological-Record* literature, might be considered the only serious weakness of the publication. For instance, a rather large number of species or potential species that are well known in current literature, e.g. *Gammarus oceanicus* Segerstrale, 1947, Kinne, 1954; *G. salinus* Spooner, 1947, Kinne, 1954; *Rivulogammarus pulex fossarum* Koch, 1835, Arnoud, 1953; etc., are not included or are buried in synonymy. Moreover, current refinements in amphipod taxonomy are expected to make commonplace the practice of subspecific treatment of species complexes, particularly where geographically large series of specimens are available for study. It is a delight to work with a publication so free of mechanical errors; the reader assumes that the accepted standard of spelling, especially in controversial cases like Ampithoidae, Liljeborgiidae, *Gammarus camylops*, etc., is that of Stebbing (1906). The validity of taxons has been based on pertinent revisionary work of the most experienced and/or most recent specialists, in some cases on very recently published or even unpublished sources, and on the author's own leanings toward the "splitter's" viewpoint. The result points up the present uneven calibre of amphipod systematics. A pertinent case is Barnard's decision to adopt (with minor reservations) Bulycheva's recent (1957) but untested revision of the Talitridae. This work ele-

vates the whole group to the status of a superfamily (Talitroidea) within which are created three (new) families based essentially on marine, fresh-water, or terrestrial tendencies of the component species. The *Index* raises several other such problems in amphipod systematics; Barnard hopes that attention will be drawn to these problems, and interest in their solution generated. Finally, it is to be hoped that this fine compilation will stimulate the production of much-needed catalogues of the other amphipod suborders (Caprellidae, Hyperiidea, Ingolfiellidea) which, because of their relatively small size, might conveniently be combined under one cover.

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